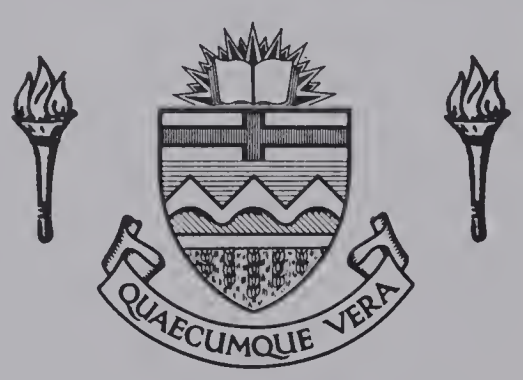

THE UNIVERSITY OF ALBERTA

TAXONOMY OF TRYPANOSOMES (PROTOZOA: TRYPANOSOMATIDAE) PARASITIC IN SOME SPECIES OF SPERMOPHILUS (RODENTIA: SCIURIDAE)

by

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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Taxonomy of Trypanosomes (Protozoa: Trypanosomatidae) Parasitic in Some Species of Spermophilus (Rodentia: Sciuridae)" submitted by Donald Frederick James Hilton in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

ABSTRACT

During the summers of 1969-71 554 ground squirrels belonging to six species (115 Spermophilus columbianus, 46 S. franklinii, 13 S. lateralis, 327 S. richardsonii, 20 S. tridecemlineatus, and 33 S. undulatus) were sampled for trypanosomes. Natural infections were recorded in all but S. lateralis.

In 1969 and 1970 the prevalences of infection were approximately equal within, but varied between, each species of ground squirrel. In 1971 the prevalences of infection increased for all host species sampled. Trypanosomiasis was detected in twice as many ground squirrels when the hematocrit centrifuge technique was used for diagnosis instead of stained thin blood films.

In S. richardsonii the prevalences of infection varied from month to month but showed the same trends in both 1969 and 1970. Prevalence was lowest in May and highest in June. It is suggested that susceptible juveniles accounted for the high prevalence in June.

Natural transmission of trypanosomes has not been demonstrated, but on the basis of ectoparasite surveys and the work of other authors it seems likely that fleas are biological vectors both within and between species of ground squirrels.

The trypanosome strains from S. columbianus, S.

richardsonii and *S. tridecemlineatus* were experimentally transmitted to 5/6, 6/6 and 2/4 of the six host species, respectively. The strain from *S. franklinii* did not produce infections when experimentally inoculated into the other host species.

Intensities and durations of experimental infections were variable and depended upon the trypanosome strain, host species and individual. Infections were non-pathogenic.

Previously infected ground squirrels could not be reinfected with the same or a different trypanosome strain and immunity appeared to be lifelong.

Size comparisons among and within trypanosome strains from naturally and experimentally infected ground squirrels revealed that the strains from *S. franklinii* and *S. tridecemlineatus* were similar to one another but different from the other three trypanosome strains.

It is suggested that there is only one species of trypanosome, *Trypanosoma otospermophili*, present in ground squirrels of the genus *Spermophilus* in North America and that differences in size and types of infection are due to host induced variations. *T. spermophili* (present in Eurasian *Spermophilus* spp.) might be synonymous with *T. otospermophili*.

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INTRODUCTION

Protozoans of the family Trypanosomatidae constitute one of the most natural groups among the flagellates, (Superclass: Mastigophorea) since the structure and life cycles of the member genera show a gradation linking them to one another (Hoare, 1966). Classification of the family (and species of mammalian trypanosomes in particular) is as follows and has been adapted from Hoare (1964, 1966, and 1967).

Phylum: Protozoa Goldfuss, 1818; emend. Siebold, 1845

Class: Zoomastigophorea Calkins, 1909

Order: Kinetoplastida Honigberg, 1963

Family: Trypanosomatidae Doflein, 1901; emend. Grobben, 1905

Genus: Trypanosoma Gruby, 1843

A. Section: Stercoraria

Subgenus: Megatrypanum Hoare, 1964

Subgenus: Herpetosoma Doflein, 1901

Subgenus: Schizotrypanum Chagas, 1909; emend. Nöller, 1931

B. Section: Salivaria

Subgenus: Duttonella Chalmers, 1918

Subgenus: Nannomonas Hoare, 1964

Subgenus: Pycnomonas Hoare, 1964

Subgenus: Trypanosoma Gruby, 1843

Subgenus: Trypanozoon Lühe, 1906

Genus: Endotrypanum Mesnil and Brimont, 1908

Genus: Leishmania Ross, 1903

Genus: Leptomonas Kent, 1880

Genus: Herpetomonas Kent, 1880

Genus: Blastocrithidia (=Crithidia pro parte) Laird, 1959

Genus: Crithidia (=Strigomonas) Léger, 1902

Genus: Phytomonas Donovan, 1909

Of the genera listed, four (Leptomonas, Herpetomonas, Blastocrithidia, and Crithidia) are monogenetic intestinal parasites of invertebrates (especially arthropods), while the other four are digenetic parasites. The life cycle of the latter alternates between two hosts; an invertebrate which acts as an intermediate host or vector, and a vertebrate or plant in which the parasites inhabit the blood and/or tissues (Leishmania, Endotrypanum, and Trypanosoma) or the sap (Phytomonas), respectively (Hoare, 1967).

Hoare (1966) divides the genus Trypanosoma into two sections depending upon the site of development in the arthropod vector. In the Stercoraria development occurs in the mid- and hindguts and transmission to the vertebrate is contaminative via infected feces coming into contact with wounds or mucous membranes. Development in the Salivaria takes place in the mouthparts and/or salivary glands of arthropods and transmission results during the

process of blood feeding.

Trypanosomes of ground squirrels (and most other rodents) belong to the subgenus Herpetosoma and have been recorded from approximately 80 to 90 different species of rodents throughout the world (Davis, 1952). They are all very similar in morphology and are often designated as lewisi-like after the type species, Trypanosoma (Herpetosoma) lewisi (Kent) Laveran and Mesnil. These trypanosomes cannot be differentiated with certainty by morphological differences alone since there is great variation in body size even within a single host animal (Davis, 1952). Thus, most parasitologists have described as new any trypanosome found in the blood of a different host species.

My study concerns those trypanosomes found in the ground squirrel genus Spermophilus. Trypanosomes have been named from eight species of Spermophilus--four species of ground squirrels in the U.S.S.R. (nine according to Galuzo and Novinskaya, 1968) and four in North America. Although Galuzo and Novinskaya (1968) list nine species of Russian ground squirrels as hosts for trypanosomes, many of their host species are, as Ellerman and Morrison-Scott (1951) and Ognev (1963) show, subspecies of more generally accepted species. Consequently I have followed the latter authors and given subspecific status (where applicable) to Galuzo and Novinskaya's "species".

According to Galuzo and Novinskaya (1968) trypanosomes from Russian ground squirrels were first observed by Shalashnikov in 1888 from S. pygmaeus musicus Ménétries and S. suslica guttatus Pallas. In 1910, Grjuner reported trypanosomes from S. undulatus eversmanni Brandt collected at Yakutia. Laveran (1911) then gave the name Trypanosoma spermophili to the trypanosomes from these three species of hosts. In 1913 Tartakovsky described T. schalaschnicovi from S. suslica guttatus obtained near Kherson. Kol'tzov (1914) recorded trypanosomes from S. pygmaeus mugozaricus Lichtenstein and S. f. fulvus Lichtenstein caught near Ural'sk, as did Nikitin (1927) from S. s. suslica Guldenstaedt obtained at Odessa. Neither of these investigators named the trypanosomes. Bozhenko (1927) found trypanosomes in S. f. fulvus, S. pygmaeus mugozaricus, S. pygmaeus musicus, and S. s. suslica trapped in the area between the Urals and the Volga river. On the basis of successful cross transmission experiments he regarded all four strains as T. spermophili. Bozhenko was unable to infect "white mice, guinea pigs, hares, skunks, grey rats, dogs, cats, and camels." Zasuhkin (1936) observed trypanosomes in S. f. fulvus, S. p. pygmaeus Pallas, and S. s. suslica collected from southwest R. S. F. S. R. (Russian Soviet Federative Socialist Republic). Later,

Zasukhin (1946) reported trypanosomes in S. rufescens from the same locality. However, S. rufescens is probably not a valid species since Zasukhin was the first (and only) author to use this specific epithet and it is not listed in either Ellerman and Morrison-Scott (1951) or Ognev (1963). Zasukhin assigned all these trypanosomes to T. spermophili in accordance with the view of Bozhenko. Galuzo and Novinskaya (1968) reported trypanosomes from S. f. fulvus, S. pygmaeus brevicauda (=S. intermedius) Brandt, and S. p. pygmaeus. They conducted cross transmission experiments among these three hosts as well as with "white mice, guinea pigs, hares, dogs, horses, sheep, goats, large and small jerboas, rabbits, moles, large gerbils, water rats, hedgehogs (large-eared), field mice, snakes, steppe turtles, toads, jackdaws, doves, domestic geese, ducks, chickens, and pigeons." Only the ground squirrels became infected. Galuzo and Novinskaya followed Bozhenko and considered all three trypanosome strains as T. spermophili, even though there were minor morphologic differences among them.

North American parasitologists have described four species of trypanosomes from the genus Spermophilus. Wellman and Wherry (1910) described Trypanozoon otospermophili from S. (=Otospermophilus) beecheyi (Richardson) in California. Laveran (1911) assigned

this trypanosome to the genus Trypanosoma, as Trypanosoma otospermophili (Wellman and Wherry, 1910) Laveran, 1911. Watson and Hadwen (1912) described T. citelli from S. richardsonii (Sabine) collected near Lethbridge, Alberta. Becker and Roudabush (1934) described T. iowensis from S. tridecemlineatus (Mitchill) and T. hixsoni from S. franklinii (Sabine) from Iowa. They undertook limited cross transmission studies (numbers not given), but were unable to infect S. tridecemlineatus with T. hixsoni using the infected blood of S. franklinii. However, they were later able to infect these same individuals of S. tridecemlineatus with T. iowensis. These are the only known attempts of cross transmission of trypanosomes in ground squirrels in North America.

The question is thus raised as to the proper name(s) of the species of trypanosomes found in ground squirrels. If there is only a single species (as Hoare, 1966 believes), then by the law of priority, its name would be T. otospermophili. If there is one species in North America and another in Eurasia, the North American one would be T. otospermophili and the Eurasian one T. spermophili. Levine (1965) states that the four North American species probably belong to one species but, in the absence of detailed cross transmission studies, it is better to

retain the names originally assigned to them.

The life cycles and vectors of the trypanosomes in ground squirrels have not been determined either in the U.S.S.R. or North America. Fleas are vectors for the following related trypanosomes: T. evotomys Watson and Hadwen of bank voles, Clethrionomys glareolus (Schreber) (Molyneux, 1969b); T. grosi Laveran and Pettit of long-tailed mice, Apodemus sylvaticus (L.) (Molyneux, 1970); T. lewisi (Kent) of Norway rats, Rattus norvegicus (Berkenhout) (Minchin and Thomson, 1915); T. microti Laveran and Pettit of field voles, Microtus agrestis (L.) (Molyneux, 1969a); T. musculi (=duttoni) Kendall of house mice, Mus musculus (L.) (Molyneux, 1970); T. nabiasi Railliet of European rabbits, Oryctolagus cuniculus (L.) (Grewal, 1957); T. neotomae Wood of Portola wood rats, Neotoma fuscipes annectens Elliot and San Diego wood rats, N. f. macrotis Thomas (Wood, 1936); and T. zapi Davis of jumping mice, Zapus princeps alleni Elliot (Davis, 1952).

In these examples the fleas ingest the trypanosomes while taking a blood meal from the host. The trypanosomes develop in the flea's alimentary canal (Molyneux, 1970), then transform into metacyclic trypanosomes which are infective to the definitive host through ingestion of the flea or its feces, or by having crushed infected fleas or feces rubbed into mucous membranes or breaks

in the skin.

Two main types of reproduction occur in the vertebrate host (Molyneux, 1970). In T. grosi, T. lewisi, and T. musculi reproduction is by division of epimastigotes (terminology according to Hoare and Wallace, 1966) in the bloodstream. In contrast, division occurs in the amastigote stage in the spleen and lymphoid tissues with T. nabiasi, lung and heart capillaries with T. zapi, and lymphoid tissue with T. evotomys and T. microti. In species reproducing in the tissues, the dividing forms are very scarce and difficult to see (Molyneux 1969a & b), and have not yet been found for the un-named trypanosome from collared lemmings, Dicrostonyx groenlandicus (=torquatus) (Traill) (Quay, 1955) or for T. neotomae (Wood, 1936). Molyneux (1969a & b) found dividing forms of T. evotomys and T. microti in smears of fresh appendix lymphoid tissue but could not detect them in sections.

The major objective of this study was to determine the taxonomic status of trypanosomes parasitic in five species of ground squirrels of the genus Spermophilus in North America. It was hoped that the results obtained would provide an indication of the type of taxonomic relationships that exist among trypanosomes of ground squirrels.

TAXONOMIC CRITERIA

The lack of sexual reproduction in many protozoans presents special problems in the differentiation of species. Thus, the definition of a species as: "groups of actually (or potentially) interbreeding natural populations which are reproductively isolated from other such groups" (Mayr, Linsley, and Usinger, 1953) has no application in a group such as the Trypanosomatidae. Flagellates of this family reproduce by various asexual methods (usually some form of fission). As a consequence, parasitologists attempting to separate species have had to rely on such characters as morphological dissimilarity, host and/or vector specificity, types of disease (if any) produced, geographical restriction (often a consequence of host and/or vector specificity), and physiological and immunological differences (Hoare, 1966; 1967).

Species Criteria

The foremost worker in trypanosome taxonomy, C.A. Hoare, has dealt with many of these problems; in a review of trypanosome taxonomy, (Hoare, 1967), he states that allied groups which are morphologically distinct with no intergradation of characters can be regarded

as species. However, if the characters of one group intergrade or are continuous with those of another, they are regarded as subspecies of the same species. With certain reservations a similar view is held by Sonneborn (1957). He observes that (under rare circumstances) trypanosomes can lose an organelle such as the kinetoplast and once this happens, sublines will also lack the organelle. Thus, if Hoare's morphological species criterion is strictly applied, the two sublines (with and without a kinetoplast) must be considered separate species. Such a procedure has been followed in the naming of Trypanosoma equinum Voges, a dyskinetoplastic strain of T. evansi (Steel). However, Sonneborn (1957) does not agree with this procedure since a single mutational step "would surely not be acceptable as a species differential in sexual organisms, and there is no good apparent reason why this should be done in asexual organisms." In this particular example I would agree with Hoare because 1) loss of the kinetoplast is in reality loss of the central DNA-containing mass so that the kinetoplast is no longer stainable (thus dyskinetoplastic rather than akinetoplastic); 2) the DNA of the kinetoplast is a necessity for the completion of the life cycle in the arthropod vector, and therefore T. equinum can only be transmitted mechanically; 3) T. evansi is an Old World parasite, whereas T. equinum is a New World parasite, probably

introduced with imported horses during the middle of the last century, and has continued to reproduce true since its discovery in 1901 (Hoare, 1967).

Corliss (1962), Hoare (1966), and Sonneborn (1957) all caution the use of host-specificity or virulence as the sole criterion for species determination. In particular, Sonneborn (1957) points out that comparable traits in bacteria and viruses arise as single mutational steps and are inherited as single gene traits. Consequently, he objects to their use as species differentials on the same grounds as for the loss of an organelle such as the kinetoplast (but see above).

Subspecies Criteria

Trypanosomes have been separated into subspecies on morphological and biological differences (Hoare, 1966), but care must be taken because trypanosomes reproduce asexually and sublines differing in various characters can easily appear (Sonneborn, 1957). In addition, parasites (particularly protozoans) can undergo host-induced variations which are most commonly expressed as size differences (Mayr, Linsley and Usinger, 1953). Corliss (1962) does not believe subspecies should be described among the Protozoa because knowledge is so limited concerning factors which serve as bases for precise characterization of such subdivisions. However, Hoare (1966), suggests that some populations of trypanosomes should be

considered as subspecies (even on the basis of host-specificity) for practical purposes alone. He notes that three species, T. brucei Plimmer and Bradford, T. gambiense Dutton, and T. rhodesiense Stephen and Fantham were known and used for many years by veterinary and medical workers, but are now considered to be three strains of one species, T. brucei. However, since one strain is host specific and the other two cause distinct types of disease, Hoare states that, for the convenience of medical and veterinary researchers, the strains should be given subspecific status (i.e. T. b. brucei, T. b. gambiense, and T. b. rhodesiense).

Infrasubspecific Categories and Criteria

With certain exceptions, such as the example noted above, Hoare (1943, 1952, 1966, 1967) has not given subspecific status to strains separable on purely biological features such as host-specificity or type of disease produced. He believes strains should be relegated to infrasubspecific categories and proposes to call them demes, with the suggestion that an appropriate prefix be attached to designate the type of deme concerned (e.g. xenodeme: host-restricted population; nosodeme: population producing a different type of disease).

In addition, there are groups with unstable environmentally induced characters which Hoare (1943, 1952, 1966, 1967) has termed Dauermodifikationen (transient modifica-

tions) and Gilmour and Heslop-Harrison (1954) as plastodemes. This terminology is usually restricted to relapse strains in certain parasitic protozoans such as the pathogenic African trypanosomes. However, it can be applied to xenodemes which undergo various modifications if the environment (i.e. host) is naturally or experimentally changed.

In view of the above considerations, I propose to use a combination of: statistical analysis of size differences, host-specificity, intensity and duration of infection, and geographical distribution as diagnostic criteria in attempting to determine the taxonomic status of the trypanosomes present in different species of ground squirrels.

TAXONOMY AND DISTRIBUTION OF HOSTS

Ground squirrels are sciurid rodents that belong to the genus Spermophilus Cuvier, still referred to as Citellus Oken by many. Hershkovitz (1949) has shown that Spermophilus is the correct generic name. In spite of this, Ellerman and Morrison-Scott (1951) believe the name Citellus should still be employed (due to familiarity and wide usage) until a ruling is given by the International Commission on Zoological Nomenclature. I prefer to follow Hershkovitz (1949) and Hall and Kelson (1959) in using Spermophilus.

Hall and Kelson (1959) list 23 species of ground squirrels from North America. They place the six species dealt with in my study in the following subgenera: S. (Spermophilus) columbianus (Ord), S. (S.) richardsonii, S. (S.) undulatus plesius Osgood, S. (Ictidomys) tridecemlineatus, S. (Poliocitellus) franklinii, and S. (Callospermophilus) lateralis tescorum (Hollister).

The North American distributions of these six species of ground squirrels (Hall and Kelson, 1959) are shown in Figures 1 and 2. In addition, S. undulatus also has a Palaearctic distribution (Rausch, 1953) and its range overlaps those of other species of Asian ground squirrels near the upper reaches of the Ob and Irtysh rivers in south-central Asia (Ognev, 1963).

S. columbianus is a colonial species which occurs in the Canadian, Hudsonian and Arctic-Alpine Life Zones. Within these regions they inhabit low, spruce-surrounded grasslands flanking the mountains; treeless flats, rocky slopes and benches; subalpine forest glades; and alpine regions at and above treeline. *S. l. tescorum* is a solitary species, individuals of which inhabit the same life zones as do those of *S. columbianus*, often at higher elevations. *S. franklinii* and *S. tridecemlineatus* are both solitary species and occur in the Transition and Canadian Zones. However, *S. franklinii* is restricted to shrubby and wooded regions, while *S. tridecemlineatus* occurs only in short and long grass prairies. *S. richardsonii* is colonial and restricted to the treeless plains of the upper Sonoran, as well as prairies and parklands of the humid Transition Zones. In North America, *S. undulatus* is colonial and distributed throughout portions of the Arctic and Hudsonian Zones in open and semi-open areas.

These species of ground squirrels hibernate for six to eight months of the year (July or September to March or May) depending upon the species, sex, and age.

Figure 1. North American distribution of:

S. columbianus

S. richardsonii

S. undulatus

The Province of Alberta is outlined.


160
140
120
100
80
60
40
70
60
50
40
30
120
110
100
90
600 mi.

Figure 2. North American distribution of:

S. franklinii

S. lateralis

S. tridecemlineatus

The Province of Alberta is outlined.


160
140
120
100
80
60
40
70
60
50
40
30
120
110
100
90
600 mi.

MATERIALS AND METHODS

Field Collections and Diagnosis

Ground squirrels were collected by live trapping at the localities shown in Figures 3 and 4. Individuals of *S. undulatus* were trapped 80 km northwest of Whitehorse, Yukon Territory. At Miquelon Lake, two populations of *S. franklinii* and *S. richardsonii* were sampled once per week from April to August 1970 in an attempt to determine if trypanosomes were exchanged between the two ground squirrel populations.

Blood samples were taken by tail clipping (1970, 1971) and by heart puncture from etherized animals (1969). Thin blood smears were made from each animal, air dried and stained with Wright's blood stain (Frankel, Reitman and Sonnenwirth, 1970). Smears were examined at a magnification of 200X for ten minutes. Blood from selected animals was also examined by the hematocrit centrifuge technique for detecting blood parasites (Bennett, 1962). This technique consists of filling a heparinized hematocrit capillary tube with fresh blood, sealing one end with plasticine (different colors can be used for color coding) and centrifuging in a hematocrit centrifuge for five minutes. The capillary tube is then examined at a magnification of 200X, and any trypanosomes present will be found between the plasma and buffy coat layers. This method was used as a comparison to check the efficiency

of stained thin blood films for detecting trypanosomes.

Cross Transmission Studies

Blood from infected wild-caught ground squirrels was withdrawn by cardiac puncture and mixed with an equal volume of mammalian saline (containing 3% sodium citrate by volume as an anticoagulant). Aliquots (usually 0.1 to 0.4 ml) of this blood-saline mixture were injected intraperitoneally into recipient ground squirrels. In order to determine the courses of infection, experimentally infected animals were blood sampled (by tail clipping) every one, two or three days until they had lost their infections (as determined by negative hemocytometer counts for two consecutive weeks). Blood was drawn to the 0.5 mark in a Thoma white cell blood diluting pipette, then distilled water was sucked up to the 11 mark. The pipette was rotated vigorously to thoroughly mix the blood, then introduced into a bright-lined Neubauer Improved hemocytometer. Distilled water lysed the red blood cells, leaving only white blood cells and trypanosomes (albeit distorted). The counting areas were examined using phase contrast microscopy at a magnification of 200X. The formula for determining the number of trypanosomes/cu. mm of blood was:

$$\frac{\text{trypanosomes X dilution X 10}}{\text{number of 1 mm squares counted}}$$

where the dilution was 20 and five squares were counted.

Similar studies were carried out on Sprague-Dawley

white rats and BalB-C white mice infected with the trypanosomes T. lewisi (L strain) and T. musculi, respectively. These trypanosome strains were obtained in 1970 from D. R. Lincicome of Howard University, Washington, D. C. Both species of trypanosomes are considered to be valid and for this reason comparisons were made among them and the ground squirrel trypanosomes to determine if they were demonstrably different from the latter as regards morphology, intensity and duration of infection, and host specificity.

A supply of known uninfected ground squirrels was required so that the results of experimental cross transmission could be interpreted with more confidence. Pregnant ground squirrels (S. richardsonii and S. tridecemlineatus) were collected in April 1971, dusted with louse powder (containing rotenone and abrasive particles) to remove all ectoparasites and kept in cages supplied with cotton nesting material. One-half of each litter was experimentally infected (after weaning) with the trypanosome strain from S. columbianus and the other half with the strain from S. richardsonii.

Morphological Studies

At the time blood was taken for counting, a thin smear was also made and stained with Wright's blood stain. Trypanosomes present in smears from both naturally and experimentally infected ground squirrels were drawn at

a magnification of 1000X with the aid of a Wild drawing tube. Measurements of seven trypanosome body regions (Figure 21) were determined from the drawings using a calibrated map measurer (0.125 inches=3 μm at 1000X).

Seven trypanosome body measurements were determined for all strains from both naturally and experimentally infected species of ground squirrels. Basic statistics calculated for each body measurement in all comparisons were as follows: number of hosts (NH), number of trypanosomes (NT), mean, standard deviation (S.D.) of the sample mean, estimated standard error (S.E.) of the mean, coefficient of variation (C.V.) expressed in percent, and range. Various comparisons were made among and within strains (for each body measurement) using the Student-Neuman-Keuls (SNK) analysis of variance test. The exact formulae and sequence of calculations are given in Sokal and Rohlf (1969), but essentially the test ranks the means, uses a pooled variance, and measures the differences among means in a step-wise fashion by employing the range as the critical statistic. The SNK test is computationally identical to Duncan's Multiple Range test but employs a different table of critical range values (Rohlf and Sokal, 1969). Since the means are ranked, those which are non-significant have been designated as such by drawing a vertical line beside them (see Tables in Appendix) as was suggested by Sokal and Rohlf (1969).

Correlation coefficients were computed among the seven trypanosome body measurements in natural and experimental infections to determine if the size of any particular body region was correlated with that of any other(s) within any one trypanosome strain.

All data and programs were FORTRAN IV coded on punch cards and computations were performed on an IBM 360/67 digital computer.

Hibernation Studies

Four S. richardsonii ground squirrels (experimentally infected with the trypanosome strain from the same host species) were put into hibernation (in a cold room maintained at 3°C) for a four month period beginning September 9, 1970. At the onset of hibernation three of these animals had the levels of infection indicated in Figure 6. No sampling was done during hibernation but was resumed following arousal.

RESULTS

Distribution and Prevalence of Trypanosomes

Collection localities for the five species of ground squirrels in Alberta are shown in Figure 3. There was no geographical restriction of infected animals and trypanosomiasis was usually detected at any locality from which ten or more ground squirrels were sampled.

Over a three-year period 554 ground squirrels belonging to six species were sampled for trypanosomes (Table 1). In 1969 and 1970 the prevalence of infection was approximately equal within each species but varied between them. In 1971 the prevalence of infection increased markedly for all species of ground squirrels sampled. The numbers of infected ground squirrels in Table 1 were determined by examination of stained blood smears and represent the minimum prevalence of trypanosomiasis. A more accurate assessment can be made with the more sensitive hematocrit centrifugation technique. A comparison of prevalence of trypanosomiasis in 151 ground squirrels belonging to four species examined by both the blood smear and hematocrit methods is made in Table 2. These data show that about twice as many ground squirrels (depending upon the species) are detected as having trypanosomiasis when using the more sensitive hematocrit technique.

Figure 3. Locations of Alberta collections of ground squirrels. Solid symbols represent localities at which one or more infected animals were collected.

▽ S. columbianus

□ S. franklinii

◇ S. lateralis

○ S. richardsonii

△ S. tridecemlineatus

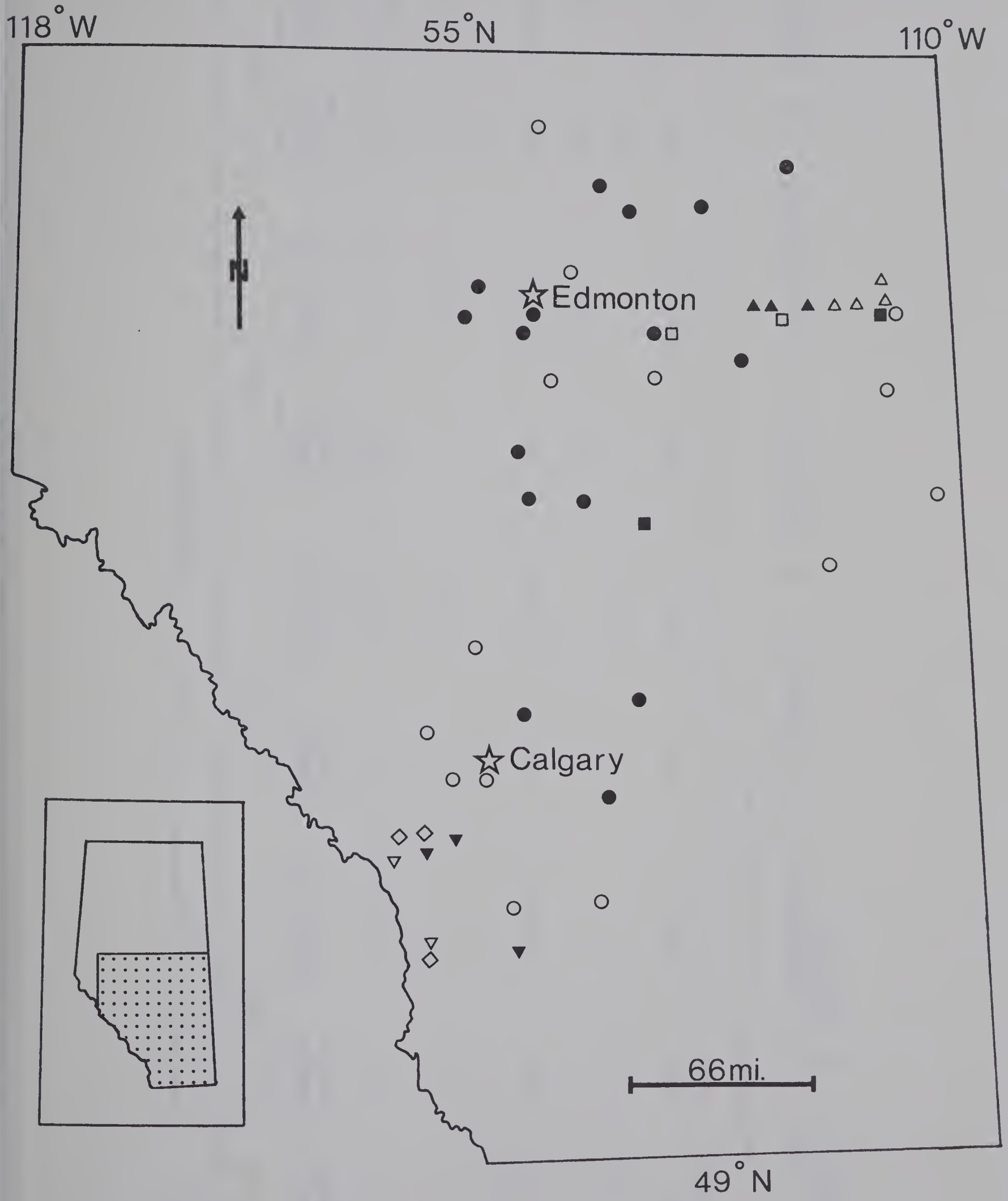

118°W
55°N
110°W
N
Edmonton
Calgary
66mi.
49°N

Table 1. Prevalence of trypanosomes in six species of Spermophilus.

Host species	1969		1970		1971		Total	
	Number examined	Number (%) infected*	Number examined	Number (%) infected	Number examined	Number (%) infected	Number examined	Number (%) infected
C	32	2(6.3)	27	2(7.4)	56	11(19.6)	115	15(13.0)
F	11	0	30	1(3.3)	5	2(40.0)	46	3(6.5)
L	4	0	9	0	-	-	13	0
R	151	20(13.3)	93	12(12.9)	83	21(25.3)	327	53(16.2)
T	-	-	5	0	15	1(6.7)	20	1(5.0)
U	-	-	33	14(42.4)	-	-	33	14(42.4)
Total	198	22(11.1)	197	29(14.7)	159	35(22.0)	554	86(15.5)

*As detected by stained blood smears.

Note: C: S. columbianus; F: S. franklinii; L: S. lateralis; R: S. richardsonii; T: S. tridecemlineatus; U: S. undulatus.

Table 2. Comparative prevalence of trypanosomiasis as detected by blood smears and the hematocrit technique.

Host species	Number sampled	Number (%) infected as detected by blood smears	Number (%) infected as detected by hematocrit method
S. columbianus	53	11(20.8)	17(32.1)
S. franklinii	5	2(40.0)	2(40.0)
S. richardsonii	78	19(24.4)	37(47.4)
S. tridecemlineatus	15	1(6.7)	4(26.7)
Total	151	33(21.9)	60(39.7)

Although the number of infected animals fluctuated from month to month, the same trends occurred in both 1969 and 1970 (Figure 5). The percent of infected S. richardsonii ground squirrels varied from 8% and 17% in April of 1969 and 1970, respectively to 0% in May of both years. The number of infected animals then rose to highs of 18% and 22% in June of 1969 and 1970, respectively. Following this June peak the number of detectable infections decreased to 15% and 13% in July of 1969 and 1970, respectively followed by a further decrease to 7% and 0% in August of 1969 and 1970, respectively. Most ground squirrels were in hibernation by the end of August.

Wild ground squirrels could not be sampled during hibernation. Trypanosomes did survive in detectable numbers in 2/3 ground squirrels kept in experimental hibernation for four months (Figure 6). The fourth ground squirrel died during hibernation.

At the Miquelon Lake study area (Figure 4) 36 individuals of S. richardsonii from area A were sampled a total of 81 times from April 28 to August 25, 1970. Of these 36 animals, eight (22.2%) were infected. In addition, 22 of the 36 animals were sampled two or more times at weekly intervals (if possible). Six of the 22 were infected but only one was infected on two separate occasions (as determined by stained thin blood smears). Twenty-one individ-

Figure 4. Map of Miquelon Lake study area.

A field inhabited by S. richardsonii

B locality inhabited by S. franklinii

fields (grasses or alfalfa)

ponds or lake

woods

roads

buildings

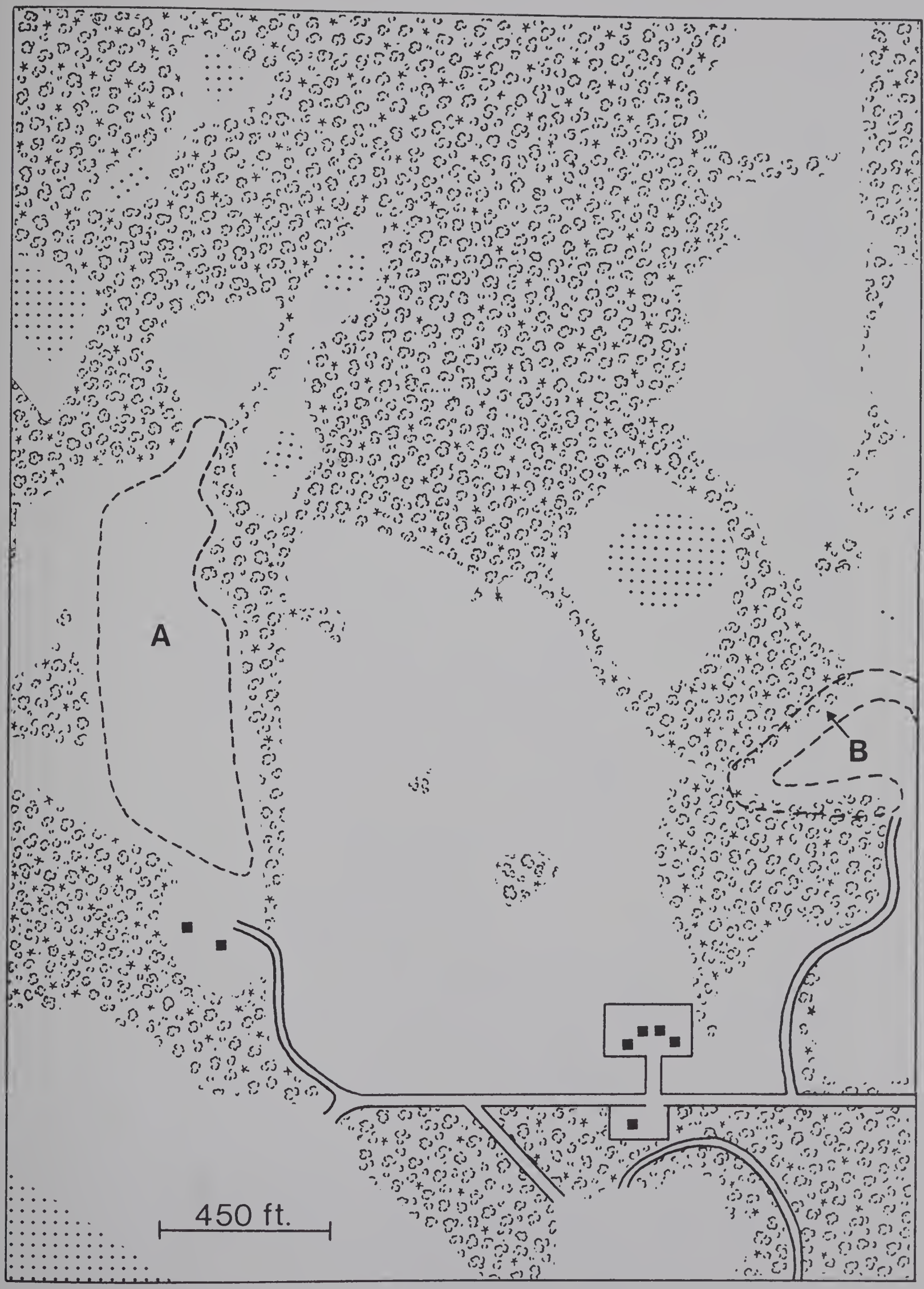

A
B
450 ft.

Figure 5. Incidence of trypanosomiasis in S. richardsonii in Alberta during the period April to August in 1969 and 1970. Sample sizes in parentheses.

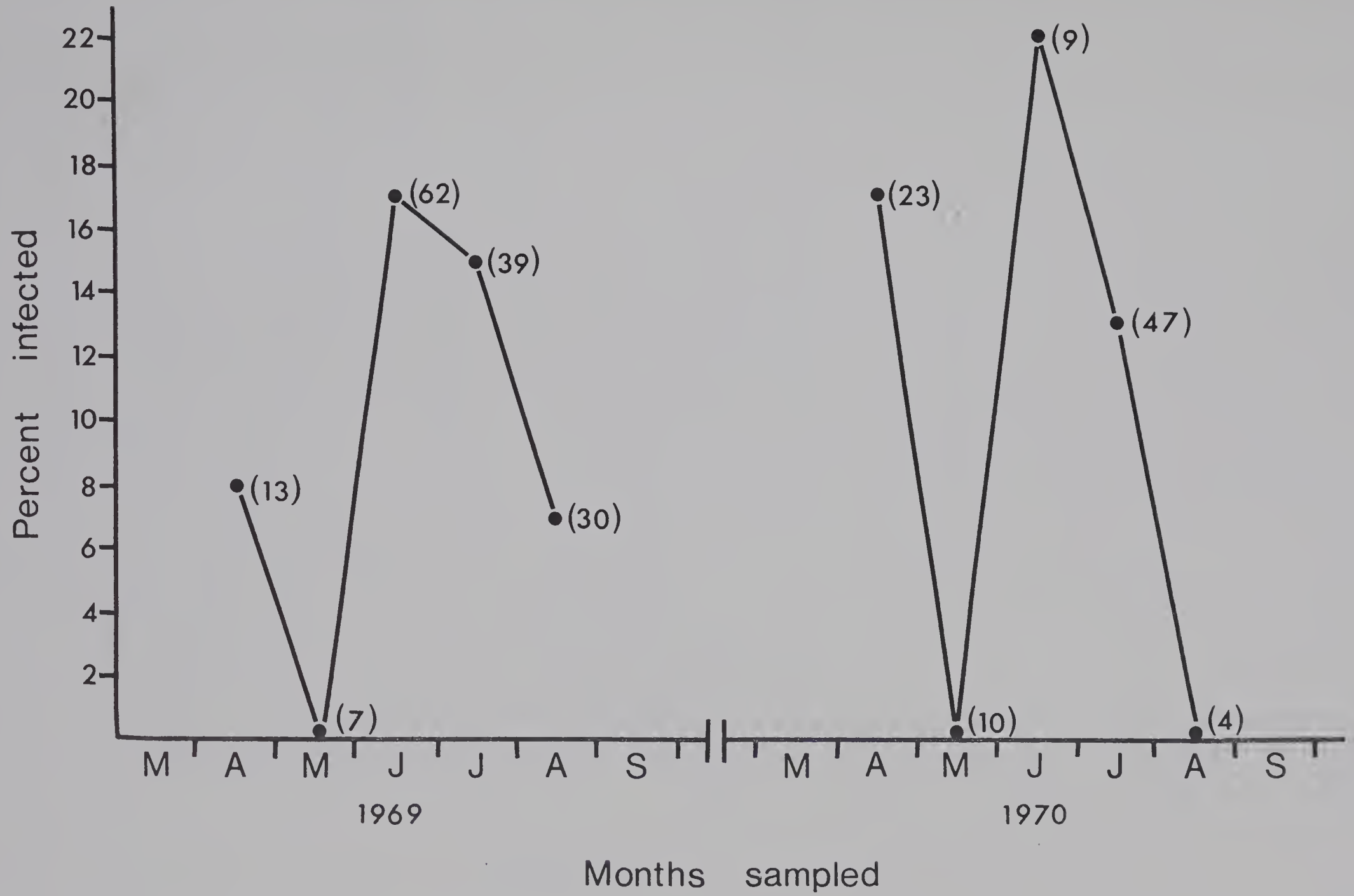
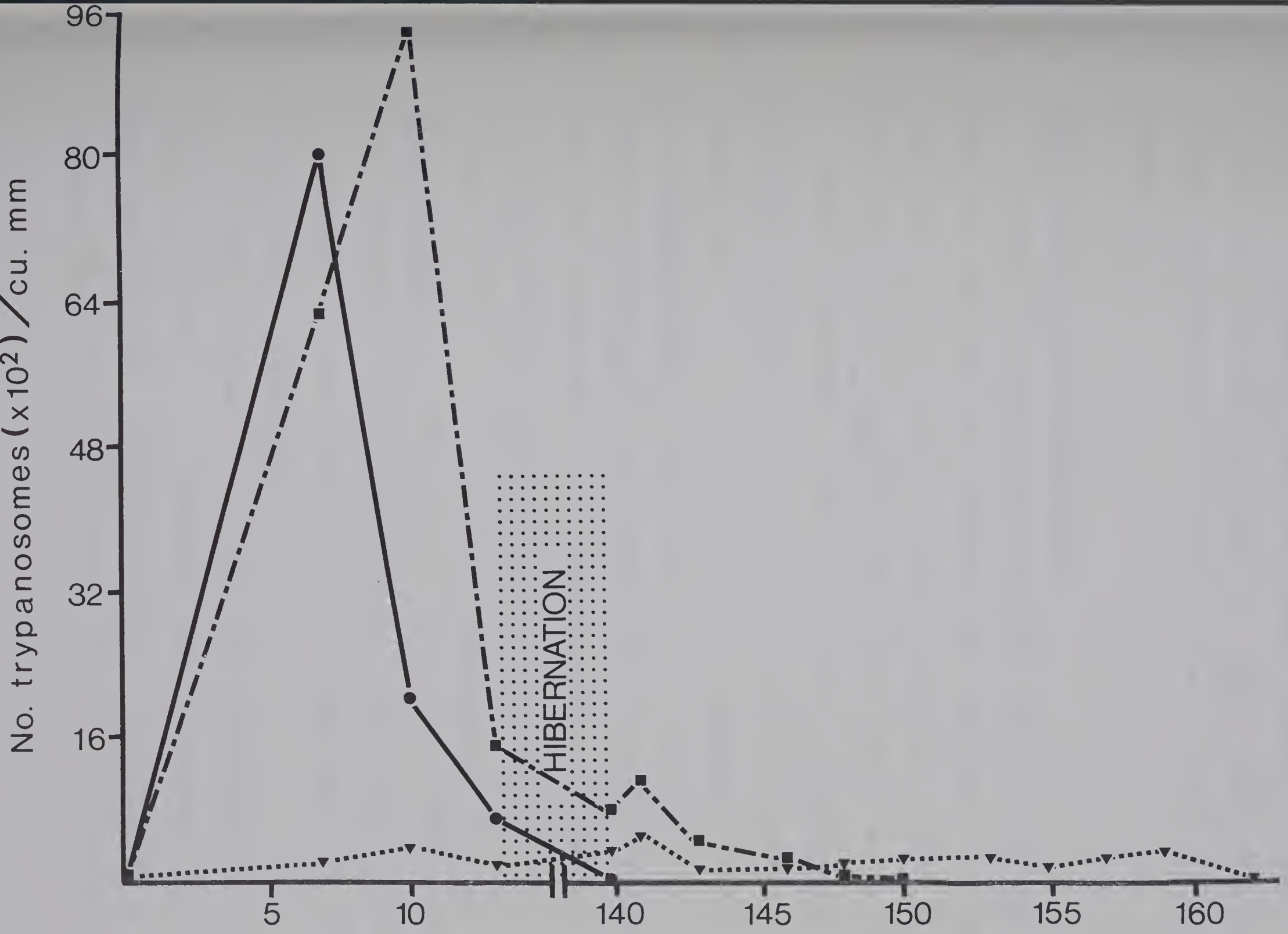

Percent infected
22
20
18
16
14
12
10
8
6
4
2
(62)
(39)
(13)
(7)
(30)
(23)
(9)
(47)
(10)
(4)
M A M J J A S
1969
M A M J J A S
1970
Months sampled

Figure 6. Effect of hibernation upon parasitaemia in three S. richardsonii.


96
80
64
48
32
16
No. trypanosomes (x10²) / cu. mm
HIBERNATION
5
10
140
145
150
155
160
Days after inoculation

uals of S. franklinii from area B were sampled a total of 52 times from May 9 to August 10, 1970. None of these animals was infected at any time, nor were any tested for susceptibility.

Host Specificity of Trypanosomes

Strains of trypanosomes from four species of ground squirrels were used experimentally to inoculate wild-caught individuals of six species of ground squirrels (Table 3). The strain from S. franklinii was the only one that failed to produce infections. The strain from S. richardsonii produced infections in all species of hosts. In heterologous hosts this varied from 2/12 S. undulatus to 5/5 S. tridecemlineatus, respectively. This compares with 20/30 S. richardsonii that became infected when inoculated with the trypanosome strain from the same host species. In a few instances (5/38) squirrels which could not be infected with the strains from S. franklinii or S. tridecemlineatus were successfully infected when reinoculated with the strain from S. richardsonii. This did not occur in the case of 13 squirrels initially inoculated with the strain from S. columbianus.

Of the juvenile (6 to 7 weeks old) ground squirrels born and reared in the laboratory (and known never to have been infected), 16/22 and 22/22 S. richardsonii developed infections after inoculation with trypanosome

Table 3. Results of experimental cross transmission experiments.*

Inoculum source	Recipient species					
	C	F	L	R	T	U
S. columbianus	5/16**(0/3)†	0/1	1/1	0/7(0/4)	1/7(0/5)	2/3(0/1)
S. franklinii	0/1(1/1)	-	-	0/10(1/10)	0/2(0/1)	0/2(0/2)
S. richardsonii	11/22	3/15	5/9	20/30	5/5	2/12
S. tridecemlineatus	2/15(2/10)	0/3(0/3)	-	1/15(1/9)	-	0/1(0/1)

*Table lists results of inoculations into wild-caught ground squirrels presumed to be negative. Naturally infected animals were used as sources of inoculum.

**Number of individuals that became infected/number of individuals inoculated.

†Figures in parentheses are number of hosts that did not develop an infection the first time but did so after being reinoculated with blood from naturally infected individuals of S. richardsonii (number of individuals that became infected/number of individuals inoculated).

strains from S. columbianus and S. richardsonii, respectively. All the infections initiated with the strain from S. richardsonii were very heavy (subjective measurement) while those induced by the S. columbianus trypanosome strain were very light. Reinoculation (with the S. richardsonii trypanosome strain) of the six ground squirrels which had not become infected with the strain from S. columbianus resulted in all six developing heavy infections.

Similarly, 7/9 and 9/9 juvenile (laboratory reared) S. tridecemlineatus developed infections after inoculation with trypanosome strains from S. columbianus and S. richardsonii, respectively. The two S. tridecemlineatus that did not develop an infection with the S. columbianus trypanosome strain were not reinoculated. Although infections initiated with the S. richardsonii trypanosome strain were heavier than those induced with the strain from S. columbianus, the differences were not as marked as those that occurred in the S. richardsonii juveniles.

Ten white rats and 10 white mice that were inoculated with the trypanosome strain from S. richardsonii did not develop parasitaemias. Six each of these same rats and mice were later inoculated with the trypanosomes T. lewisi and T. musculi, respectively. All developed infections.

All ground squirrel individuals that had lost their

Table 4. Long term immunity to trypanosome infection.

Host	First inoculation				Second inoculation		
	Days since collected	Days since infection last detected	Inoculum source	Results	Days since infection last detected	Inoculum source	Results
C	+*	330	F	-			
L	6		C	+	300	R	-
R	+	1	R	-			
R	110		R	+	235	T	-
R	30		R	+	200	T	-
U	+	1	R	-			
U	+	255	F	-			
U	+	255	C	-			
U	+	255	T	-			

*Plus signs in this column represent ground squirrels which were naturally infected when collected. Thus, the first inoculation into these individuals is equivalent to a 'second' inoculation as far as interpretation of results is concerned.

natural or experimental infections were refractory to reinfection with the same or other trypanosome strains (Table 4).

Eight naturally infected S. undulatus and eight experimentally infected S. richardsonii (two with the S. richardsonii and six with the S. columbianus trypanosome strains) were reinoculated (with the S. richardsonii trypanosome strain) once during the course of their infections. The times of inoculation varied from the increase phase until just prior to termination of the infection (see Figure 11 for infection stages). No animal developed a detectable super-infection.

Intensity and Duration of Parasitaemia in Experimental Infections

The prepatent period (as determined by stained thin blood smears) varied from two to ten days with the average for each host species as follows: S. columbianus and S. franklinii (7); S. lateralis, S. richardsonii, S. tridecemlineatus, and S. undulatus (6). These differences are not statistically significant (p=0.05). Both the T. lewisi and T. musculi trypanosome infections of white rats and white mice, respectively became patent on the third day after inoculation. This time interval difference of three to four days between the trypanosome infections of ground squirrels and those of white rats and white mice is statis-

tically significant (p=0.05)

Examples of infections produced in individuals of each species of ground squirrel after inoculation with the trypanosome strain from S. richardsonii are given in Figures 7-11. Generally, infections in S. columbianus (Figures 8, 9), S. richardsonii (Figures 7, 11) and S. undulatus (Figure 10) can be divided into three stages designated as increase, decrease and terminal (Figure 11). This is unlike infections in S. franklinii (Figures 8, 10), S. lateralis (Figure 9) and S. tridecemlineatus (Figure 7) which usually have increase and decrease stages only. The intensity and duration of infection that develops in each of these stages depends upon the host species. Thus, although there are wide individual variations, infections in individuals of all species (except S. lateralis) have intensity ranges of 200 to 3000 trypanosomes/cu. mm). Experimental infections in S. lateralis are unusual in that intensities are relatively high (about 40,000 trypanosomes/cu. mm). Durations of infection in S. columbianus and S. richardsonii are 25 to 60 days compared with 12 to 20 days for S. lateralis and S. tridecemlineatus. Generalizations about the duration of infection cannot be made for S. franklinii or S. undulatus since there are wide variations among the three infected individuals of S. franklinii and there is only one infected S. undulatus.

White rats infected with the L strain of T. lewisi usually developed infections (lethal in 7/14 rats) with

Figure 7. Intensity and duration of parasitaemia in experimental infections in S. richardsonii and S. tridecemlineatus. All squirrels received equal portions of the same inoculum from a naturally infected S. richardsonii. (Note: In Figures 7 to 12 each line represents one squirrel.)

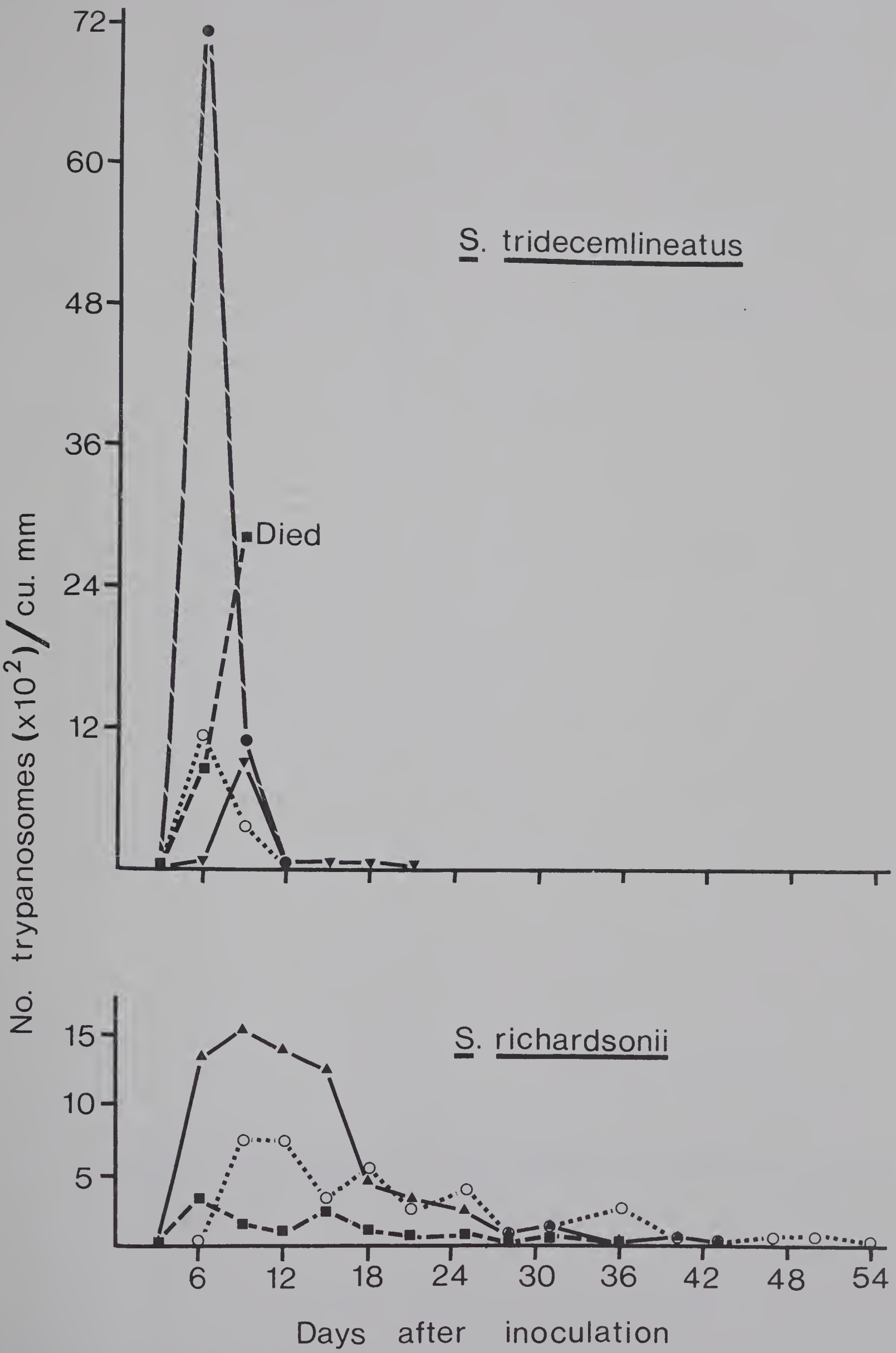

72
60
48
36
24
12
No. trypanosomes (x10²)/cu. mm
Died
S. tridecemlineatus
15
10
5
S. richardsonii
6
12
18
24
30
36
42
48
54
Days after inoculation

Figure 8. Intensity and duration of parasitaemia in experimental infections in S. franklinii and S. columbianus. All squirrels received equal portions of the same inoculum from a naturally infected S. richardsonii.

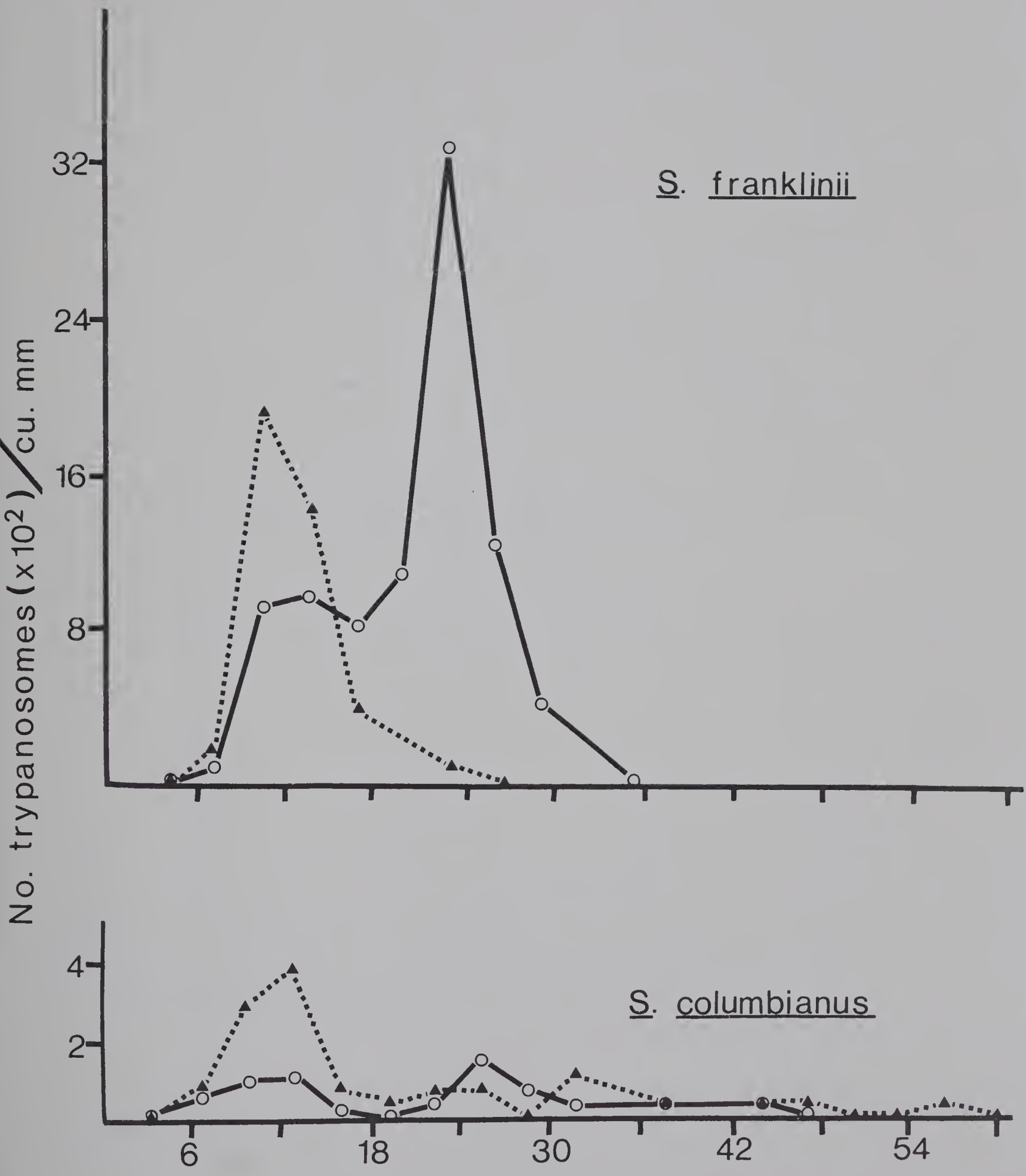

S. franklinii
S. columbianus
No. trypanosomes (x10²)/cu. mm
32
24
16
8
4
2
6
18
30
42
54
Days after inoculation

Figure 9. Intensity and duration of parasitaemia in experimental infections in S. lateralis and S. columbianus. All squirrels received equal portions of the same inoculum from a naturally infected S. richardsonii.

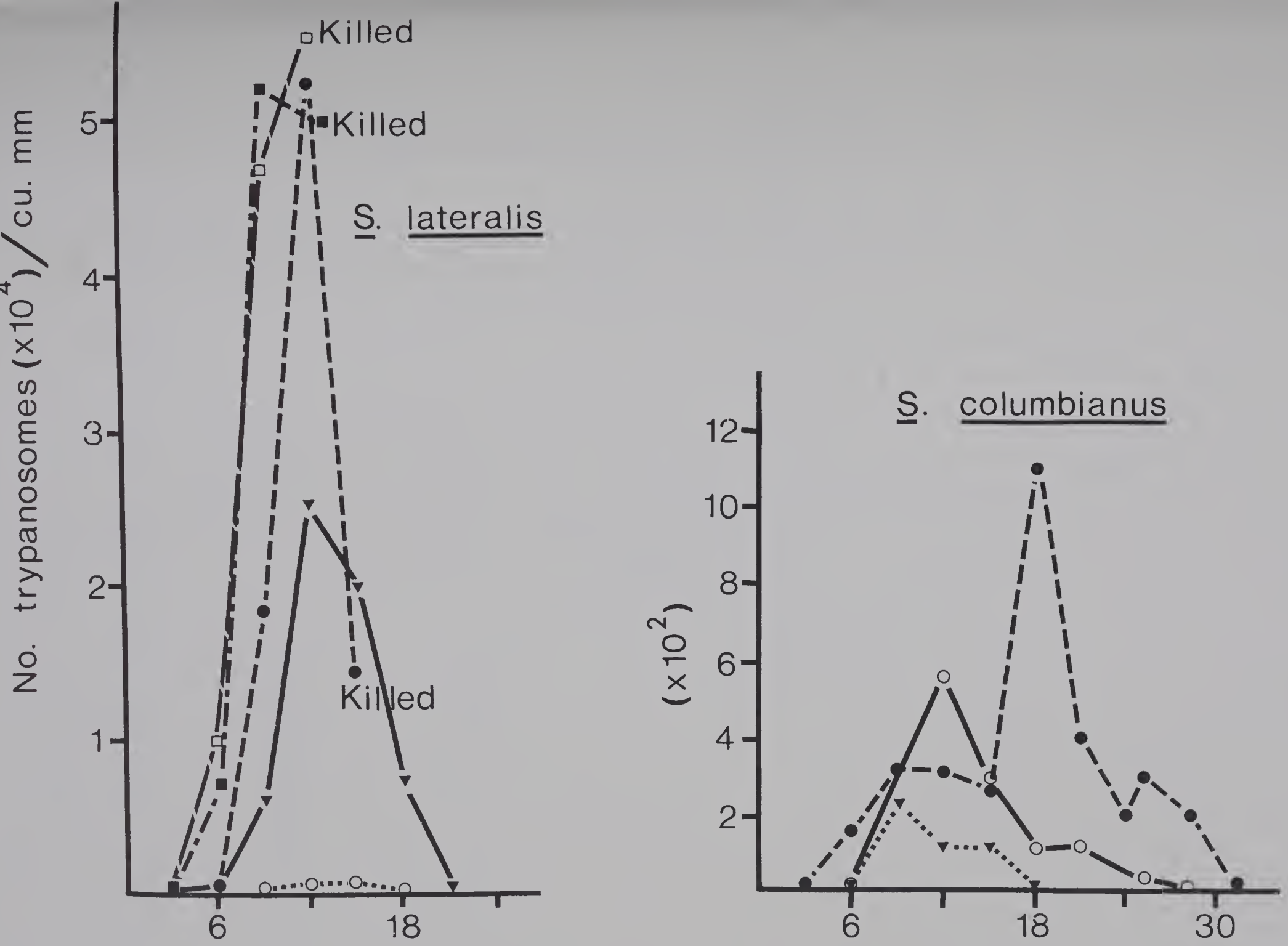

No. trypanosomes (x10⁴) / cu. mm
Killed
Killed
S. lateralis
Killed
1
2
3
4
5
6
18
S. columbianus
(x10²)
2
4
6
8
10
12
6
18
30
Days after inoculation

Figure 10. Intensity and duration of parasitaemia in experimental infections in S. undulatus and S. franklinii. All squirrels received equal portions of the same inoculum from a naturally infected S. richardsonii.

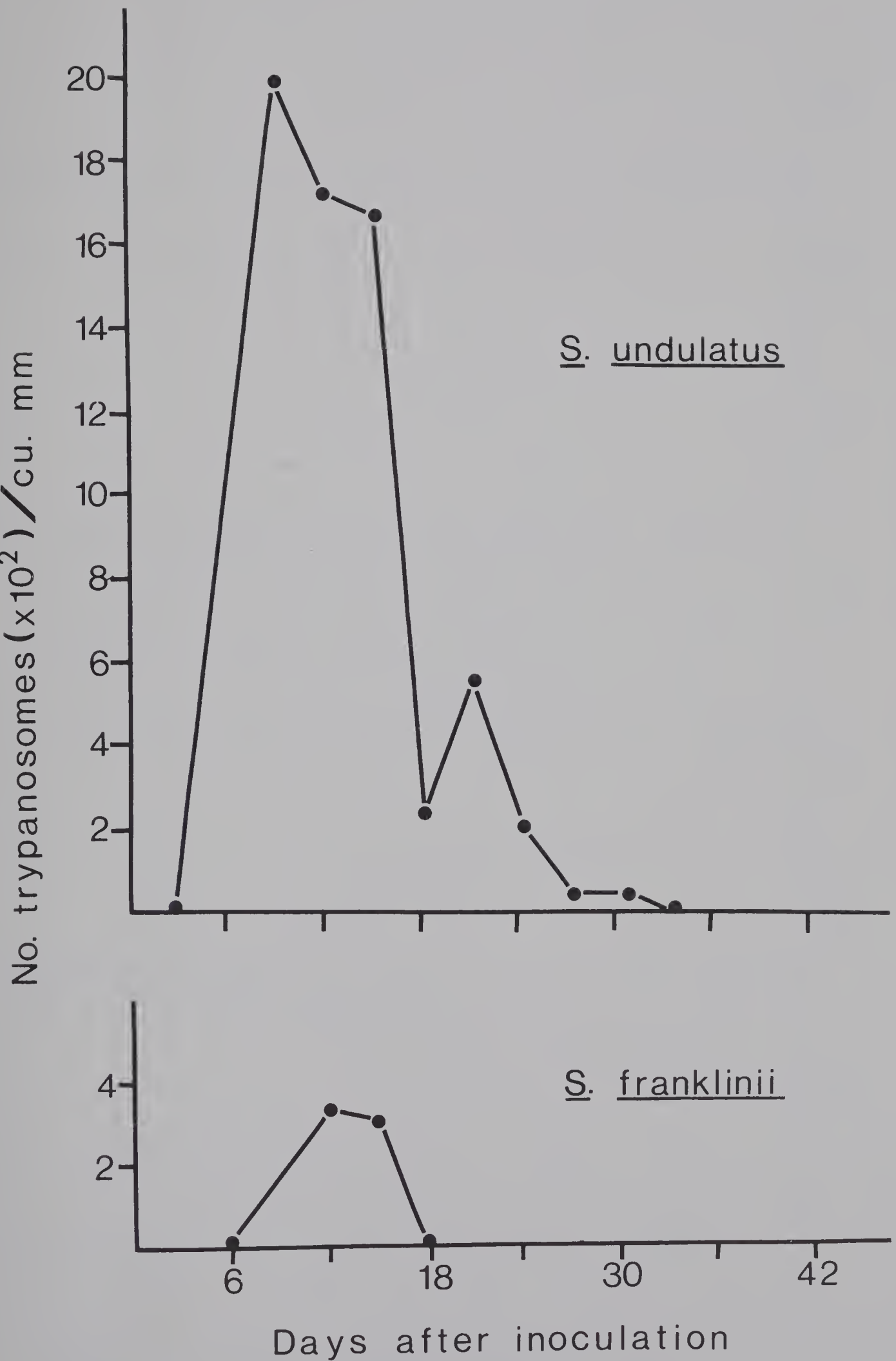

No. trypanosomes ($\times 10^2$) / cu. mm
20
18
16
14
12
10
8
6
4
2
S. undulatus
4
2
S. franklinii
6
18
30
42
Days after inoculation

Figure 11. The three phases of infection that develop during the course of ground squirrel trypanosomiasis (in this case an infection in *S. richardsonii*).

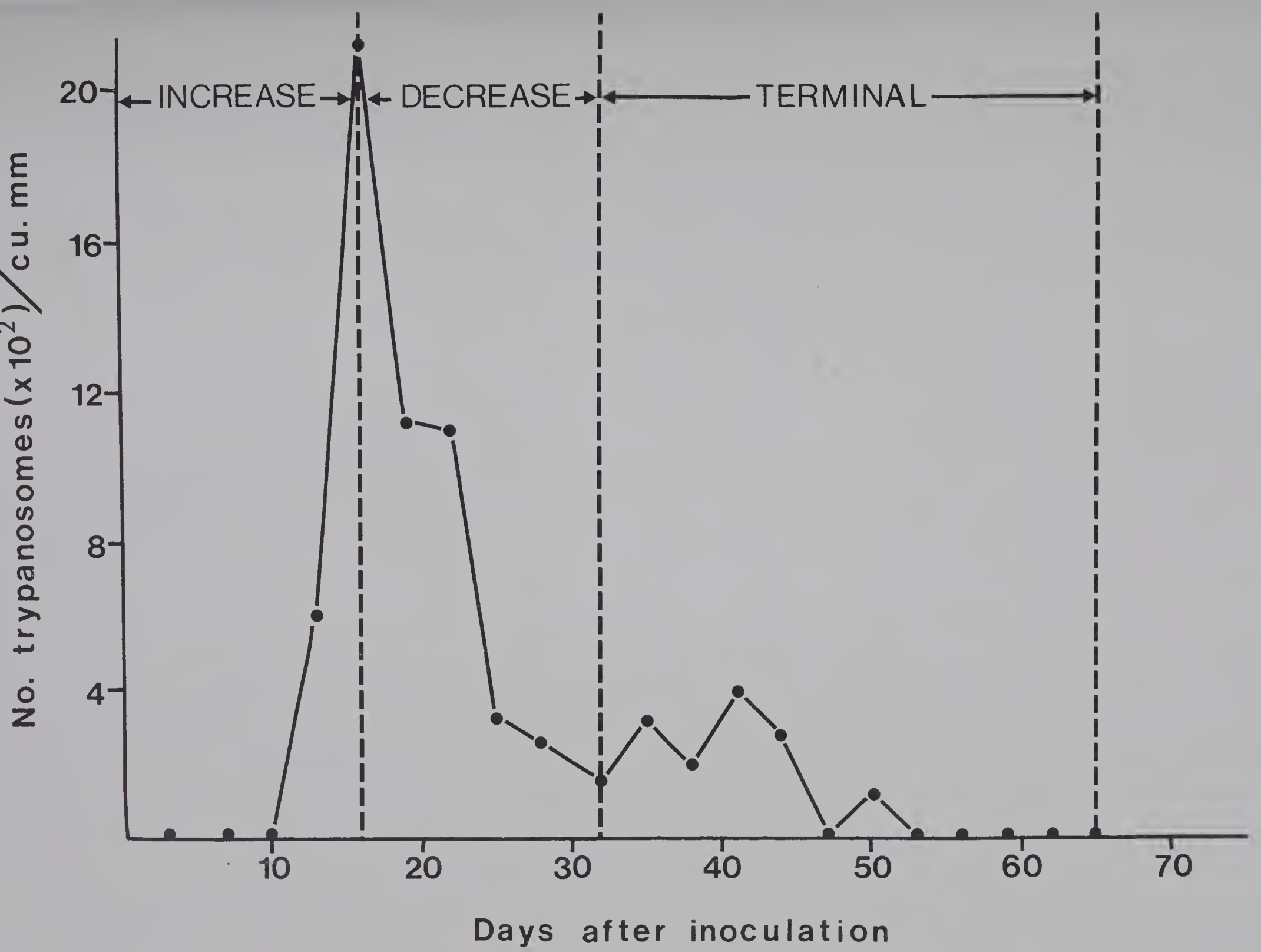

INCREASE
DECREASE
TERMINAL
20
16
12
8
4
No. trypanosomes (x 10²) / c.u. mm
10
20
30
40
50
60
70
Days after inoculation

Figure 12. Intensity and duration of parasitaemia in white rats and white mice infected with *T. lewisi* and *T. musculi*, respectively.

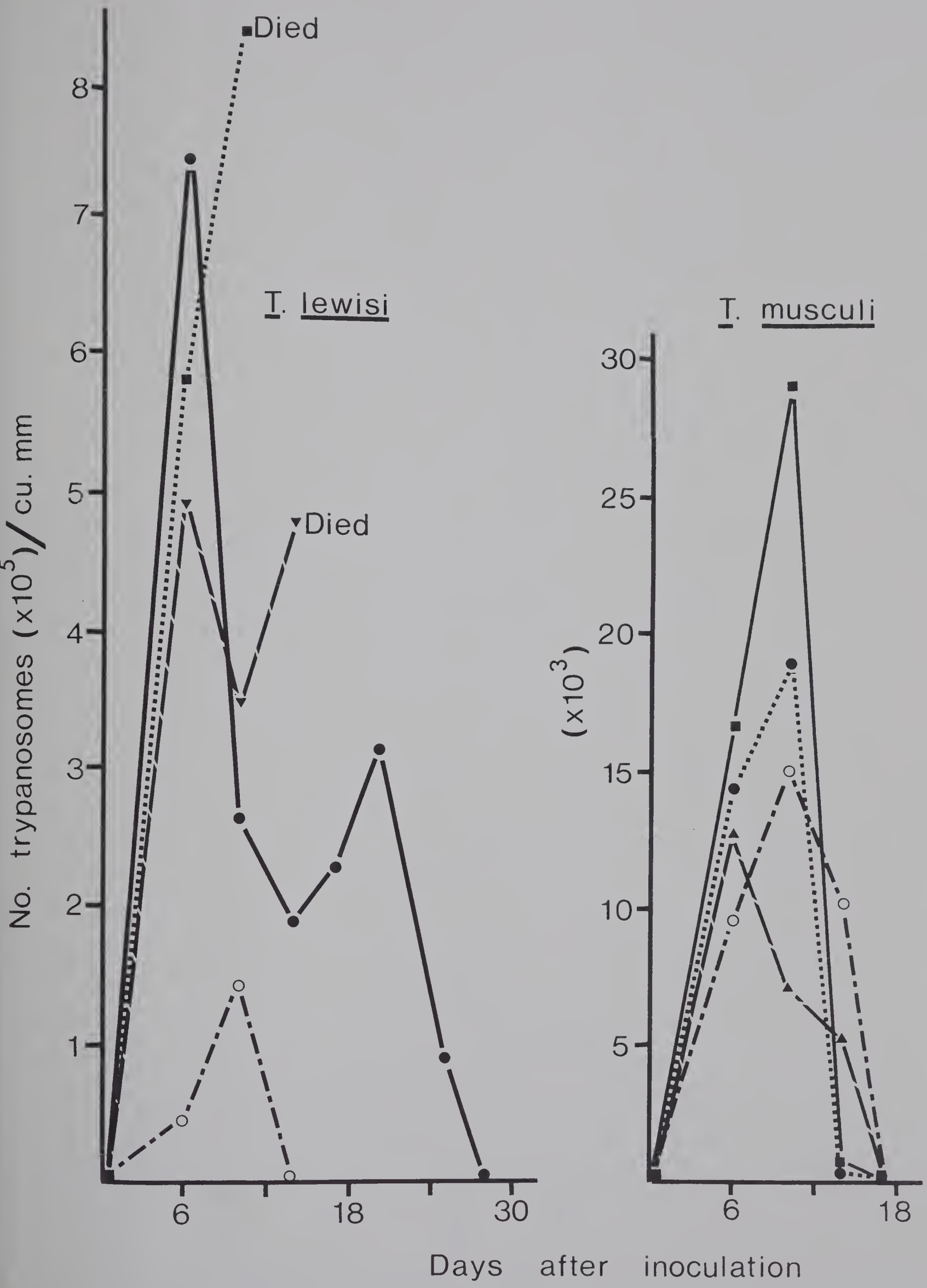
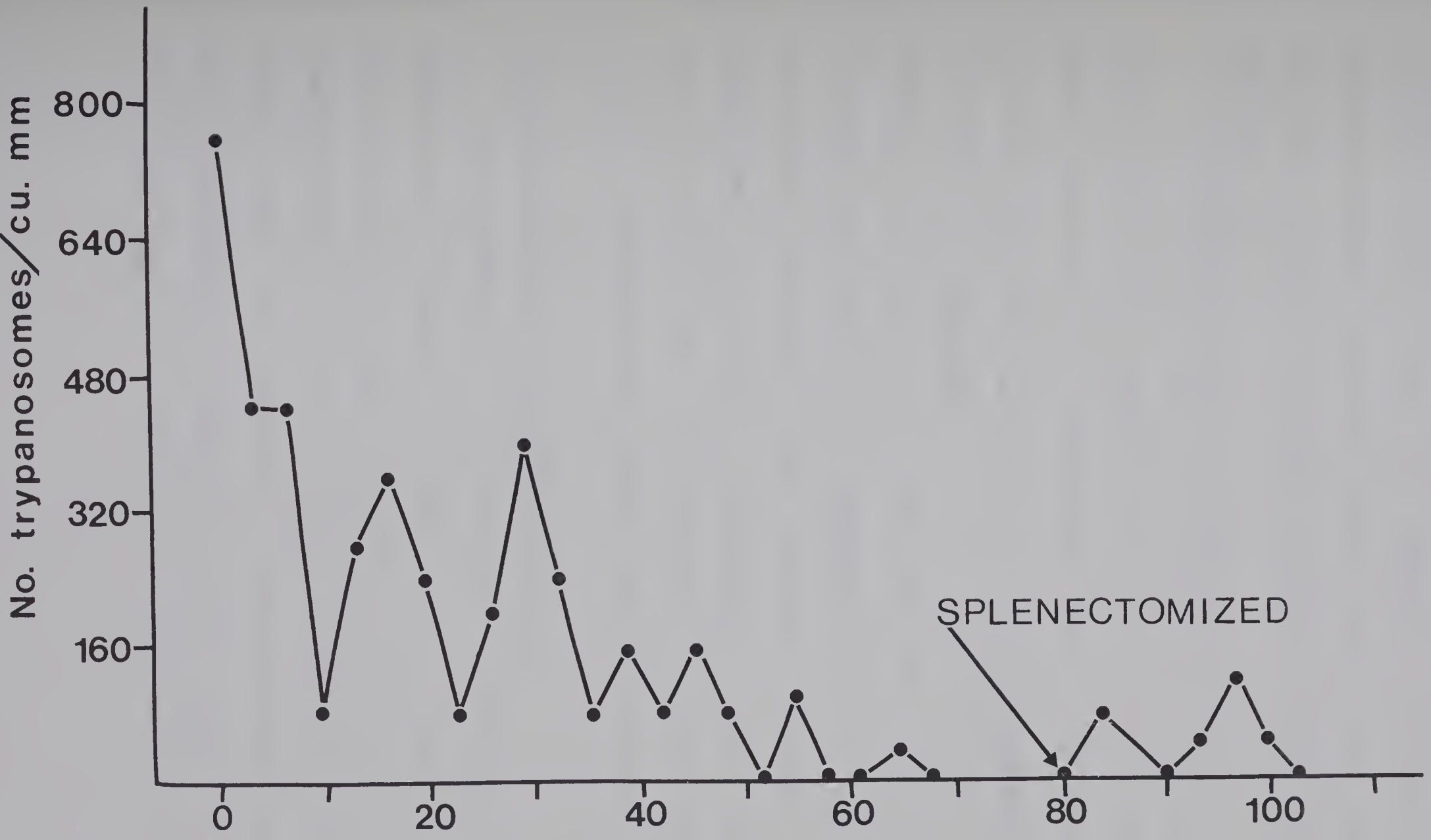

Died
T. lewisi
Died
T. musculi
No. trypanosomes (x10^5) / cu. mm
(x10^3)
8
7
6
5
4
3
2
1
30
25
20
15
10
5
6
18
30
6
18
Days after inoculation

Figure 13. Parasitaemia (in a naturally infected *S. undulatus*) as affected by splenectomy.


No. trypanosomes/cu. mm
800
640
480
320
160
0
20
40
60
80
100
SPLENECTOMIZED
Days after collecting

an intensity of about 750,000 trypanosomes/cu. mm and a duration of 15 to 25 days (Figure 12). White mice infected with a strain of T. musculi developed parasitaemias with an average intensity of 20,000 trypanosomes/cu. mm and which terminated suddenly 18 days later (Figure 12).

Trypanosomes seem to be completely removed from the host's body after completion of the terminal infection phase since only 1/12 ground squirrels splenectomized (two of each species except for one S. tridecemlineatus and three S. undulatus) at this time developed a recrudescence of parasitaemia. This occurred in a naturally infected individual of S. undulatus which had lost its countable infection 16 days previously but had a positive blood smear on the day of splenectomy (thus, the infection had not terminated). The renewed infection which developed in this animal was very short-lived (Figure 13).

Size Comparisons of Trypanosome Strains

Upon examination of the seven trypanosome body measurements compared in Tables 5 to 17 (Appendix), it can be seen that length (total) and K-MN generally have coefficients of variation (C.V.) of about 6% and 10%, respectively. The remaining five measurement regions have coefficients of variation in the range of 15% to 25% depending upon the measurement, trypanosome strain, and

type of comparison. As a result, when comparisons are made among and within trypanosome strains using only total length and K-MN there is a better chance of finding significant differences. In spite of this, many of the comparisons made with the other body measurements confirm the results obtained with length and K-MN.

In the comparisons of trypanosome size among the five species of naturally infected ground squirrels (Table 5; Figures 14, 15) it is evident that the five trypanosome strains fall into two groups. Spermophilus franklinii and S. tridecemlineatus strains form one group and are not significantly different from one another (but length and K-MN are lowest in trypanosomes from S. tridecemlineatus), but do differ significantly from strains of the other group: S. columbianus, S. richardsonii and S. undulatus. Trypanosomes from the latter group do not differ significantly from one another except for P-K and K-MN. Even in these cases, however, the three species are much closer in size to each other than they are to the S. franklinii and S. tridecemlineatus group.

It was hoped that the comparisons made in Table 6 would help determine if 1) experimental infections show the same differences between hosts as do natural infections, and 2) T. lewisi and T. musculi populations are significantly different in size from the ground squirrel

trypanosomes. When the results in Table 6 are taken together with those in Figures 14 and 15 certain trends are evident.

As is the case in natural infections, the infections in S. columbianus, S. richardsonii and S. undulatus are very closely associated (even if size differences are not always non-significant). Similarly, infections in S. franklinii and S. tridecemlineatus have lower mean values for length and K-MN than do those in the other three species. Unlike natural infections though, experimental infections in individuals of S. franklinii more closely resemble (as far as size is concerned) those in S. columbianus, S. richardsonii and S. undulatus than those in S. tridecemlineatus.

Trypanosome strains of T. lewisi (from white rats) and T. musculi (from white mice) are similar in size (for length and K-MN) to trypanosomes from experimental infections in S. tridecemlineatus (Table 6). However, the strains of T. lewisi and T. musculi are usually significantly different from one another. Based upon the data in Table 6 alone it does not appear that populations of T. lewisi and T. musculi are readily separable from the trypanosome populations of ground squirrels.

Trypanosomes from naturally infected ground squirrels are usually larger (sometimes significantly) in size than

those from experimental infections in the same host species (Tables 7, 9b, c; Figures 14, 15). The exceptions to this occur in the case of trypanosomes from S. franklinii (Table 9a) and S. tridecemlineatus (Table 8). In these host species, no matter what the inoculum source, trypanosomes from natural infections are usually smaller than, and not significantly different from (except for those in S. franklinii), experimental infections.

When a comparison is made between trypanosome populations from male and female hosts of the same ground squirrel species, those from males are often smaller (though not significantly so, except for S. franklinii as indicated in Table 10b) than those from females. With occasional exceptions this same trend occurs in both naturally (Table 10a to d) and experimentally (Table 11a to d) infected ground squirrels. In contrast, T. lewisi (Table 11e) and T. musculi (Table 11f) populations from male white rats and white mice, respectively are usually larger (not significantly) than those from females, both experimentally infected.

The trypanosome populations from two species of ground squirrels experimentally infected with equal portions of the same inoculum (Figures 16, 17; Tables 12 to 16) exhibit similar size patterns to those for the comparisons made in Figures 14, 15 and Tables 5, 6. Thus,

populations from the hosts S. richardsonii and S. tridecemlineatus (Figure 16; Table 12), and S. columbianus and S. tridecemlineatus (Figure 17; Table 16) often are significantly different from each other. In contrast, trypanosome populations from the following pairs of host species usually do not differ significantly: S. columbianus vs S. lateralis (Figure 16; Table 13); S. franklinii vs S. undulatus (Figure 17; Table 14); and S. columbianus vs S. franklinii (Figure 17; Table 15). When several trypanosome strains are inoculated into different individuals of the same host species the trypanosomes from these experimental infections within one host species are not significantly different from one another (Figure 17; Tables 7, 8).

A visual impression of the influence host individuals and species have upon size in strains of trypanosomes can be obtained from Figures 14 to 17. This is especially evident in Figure 16 which illustrates size differences among sublines of a trypanosome strain that originated from one naturally infected S. richardsonii.

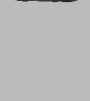
Each of the experimental infections compared in Table 6 have, in Table 17a to h, been divided into increase, decrease and terminal stages (see Figure 11) and comparisons made among these stages for each host species. There are usually no significant size differ-

ences among the stages from experimentally infected ground squirrels (Figure 18; Tables 17a to f). However, in white rats experimentally infected with the trypanosome T. lewisi, trypanosomes from the increase and decrease phases are much more highly variable (i.e. large C.V.) than the terminal phase (Figure 19; Table 17g) even though the differences among them are not statistically significant (Table 17g). The same is true for the differences between the increase and decrease phases from white mice infected with the trypanosome T. musculi, except that there is no terminal phase (Figure 20, Table 17h).

With the exception of total length, body measurements of trypanosomes from naturally (Table 18) and experimentally (Table 19) infected ground squirrels, and white rats and mice experimentally infected with the trypanosomes, T. lewisi and T. musculi, respectively (Table 20) show no significant correlations. Since P-K, K-MN, MN-A, and flagellar length together make up total length (Figure 21), they are usually positively correlated with it.

Figure 14. Comparison of mean total length for trypanosome strains from all natural and experimental infections.

natural infections



experimental infections using the trypanosome strain from S. richardsonii as the inoculum source

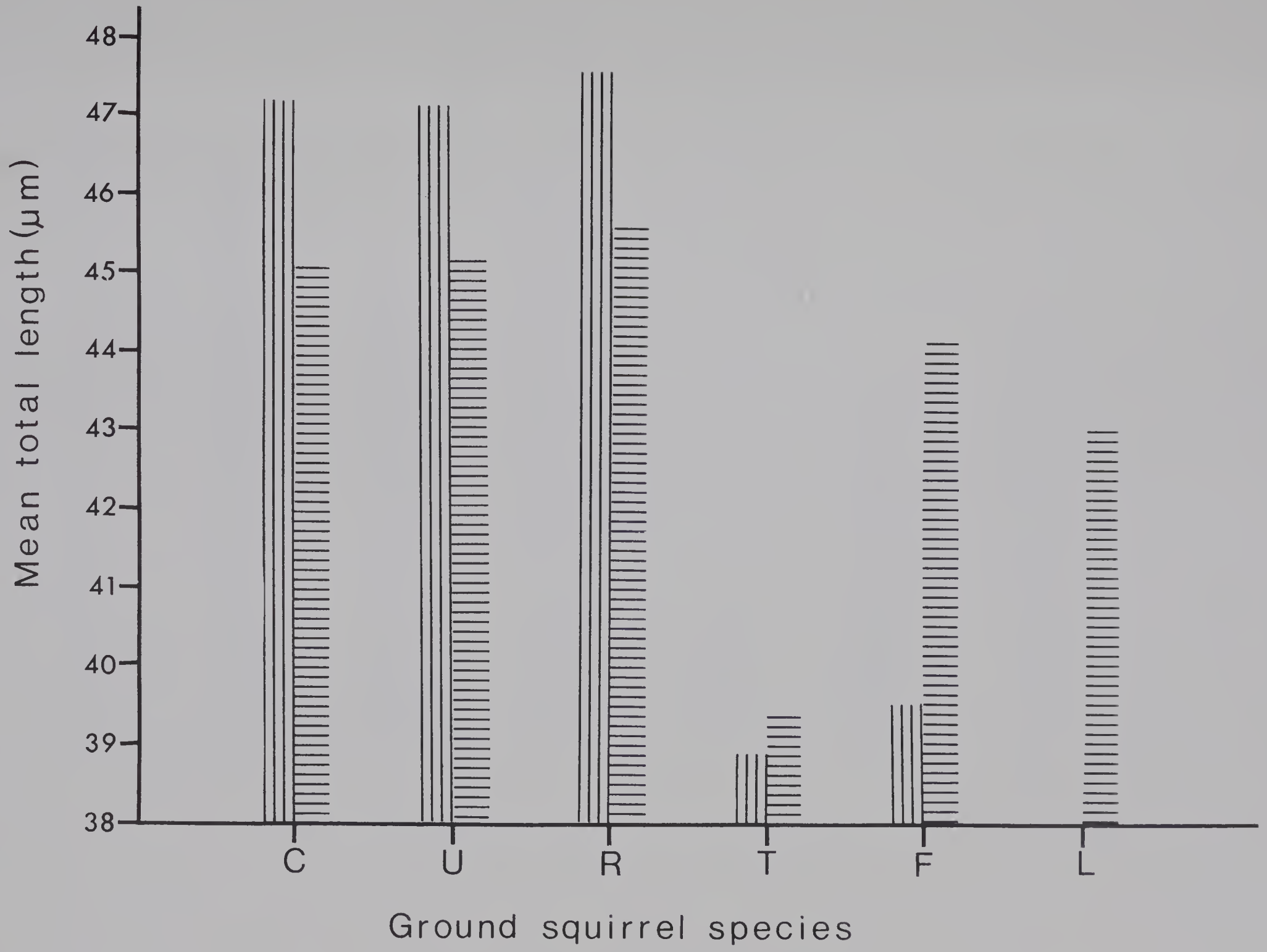

Mean total length (µm)
48
47
46
45
44
43
42
41
40
39
38
C
U
R
T
F
L
Ground squirrel species

Figure 15. Comparison of measurement K-MN for trypanosome strains from all natural and experimental infections.

natural infections

experimental infections using the trypanosome strain from S. richardsonii as the inoculum source.

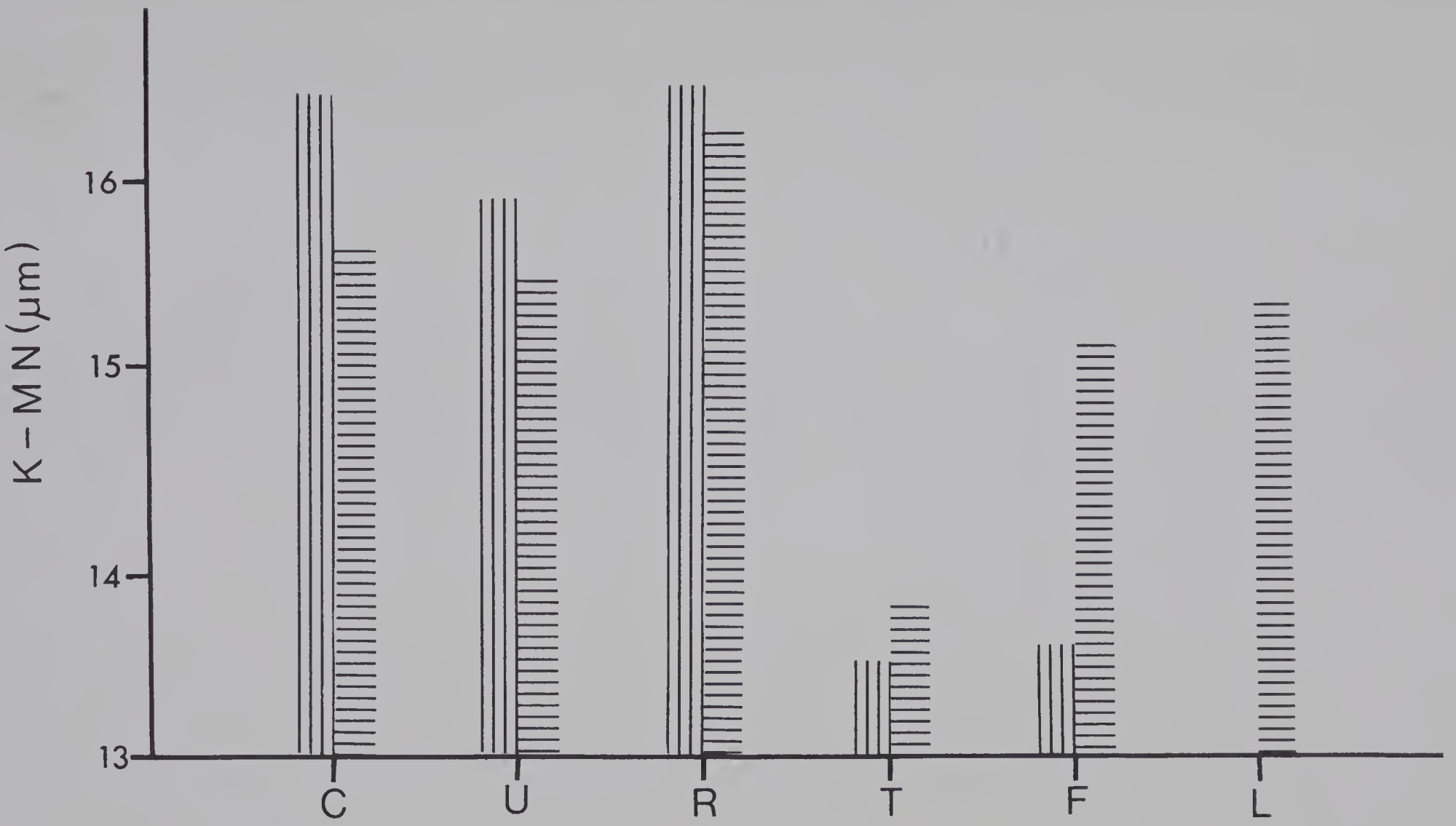

K – M N (μm)
16
15
14
13
C
U
R
T
F
L
Ground squirrel species

Figure 16. Variations in total length of trypanosomes from different host individuals and species. All infections are sublines derived from a naturally infected S. richardsonii.

Note: 1) number of trypanosomes measured are listed to the left of the range line.

2) letter to the right of the range line denotes the host species.

3) horizontal line represents range; vertical line represents mean; standard deviation of mean is represented by black and white bars on either side of mean; two estimated standard errors are represented by black bar on either side of mean.


Total length in µm
30
35
40
45
50
55
60
5 R
18 R
44 R
28 R
25 R
12 R
17 R
27 R
18 R
25 R
18 C
6 C
4 C
5 C
11 C
30 L
20 L
31 L
30 L
49 L
24 R
15 R
20 R
32 R
17 T
21 T
29 T
24 R
29 R
20 R
20 R
30
35
40
45
50
55
60

Figure 17. Variations in total length of trypanosomes from infections produced in ground squirrels of different species. Recipient squirrels in each group received equal portions of the same inoculum.

Note: symbolism employed is the same as that in Figure 16.

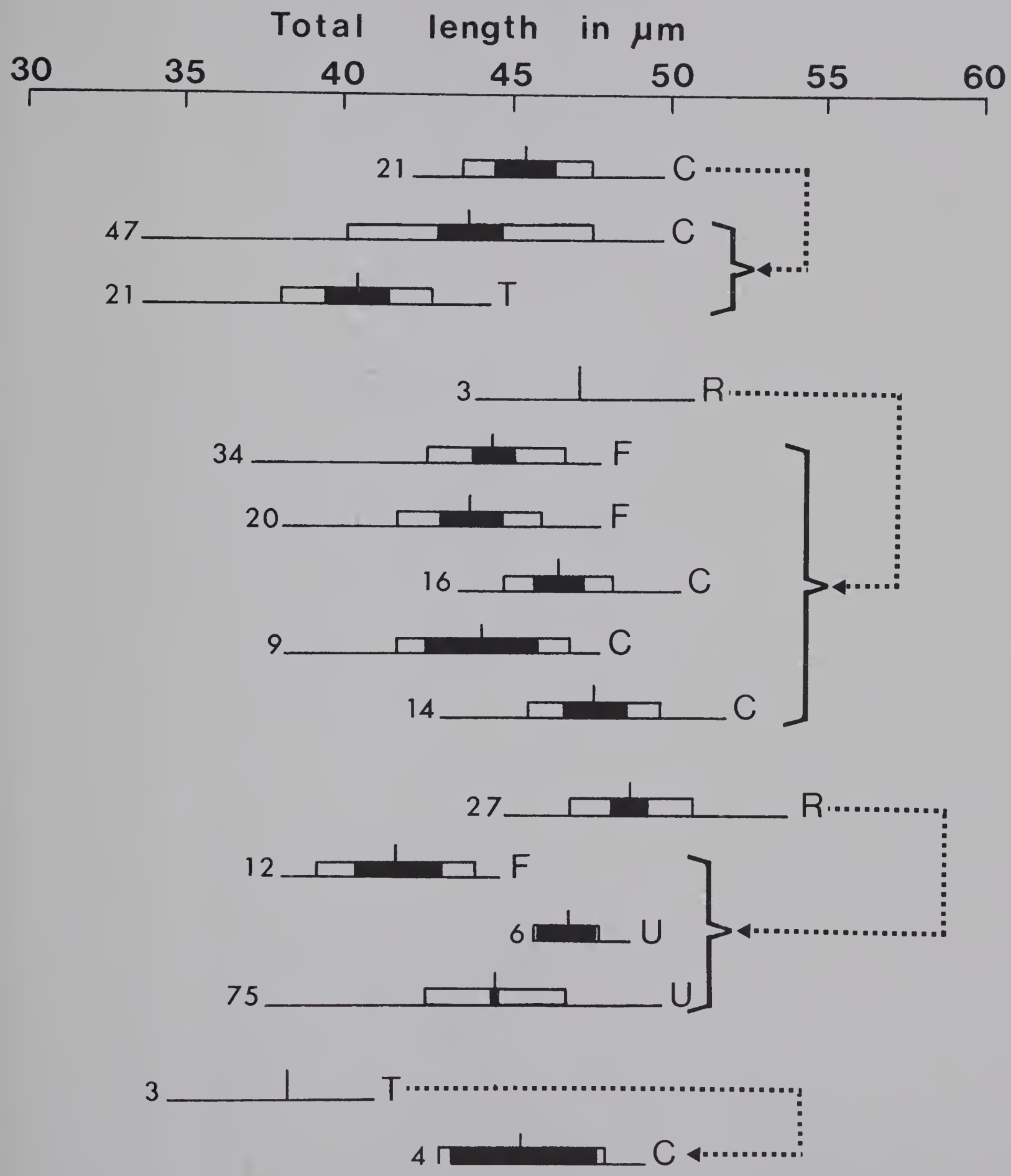
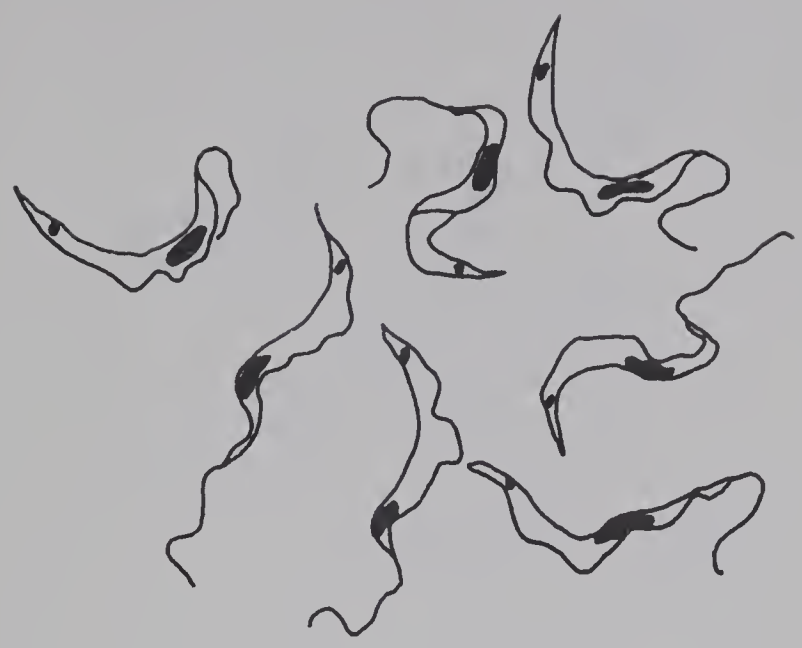
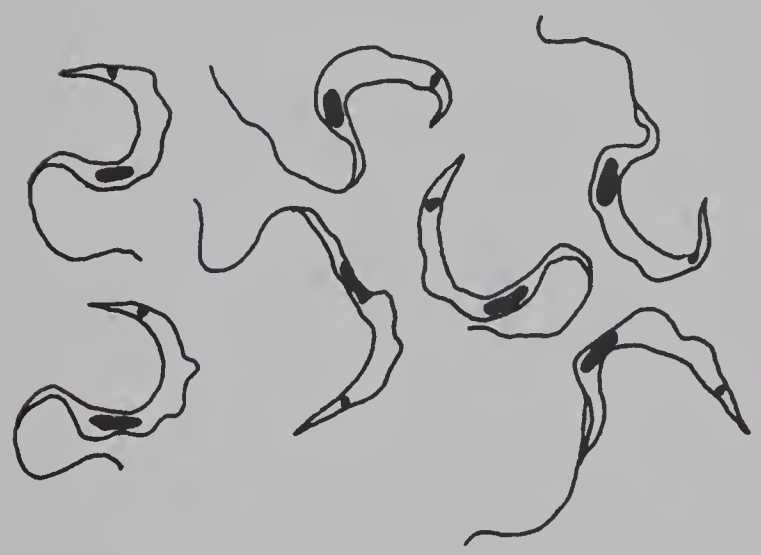

Total length in µm
30
35
40
45
50
55
60
21
C
47
C
21
T
3
R
34
F
20
F
16
C
9
C
14
C
27
R
12
F
6
U
75
U
3
T
4
C

Figure 18. Morphology of ground squirrel trypanosomes during the increase, decrease, and terminal phases of infection. Drawings were made from S. richardsonii individuals experimentally infected with the trypanosome strain from the same host species.

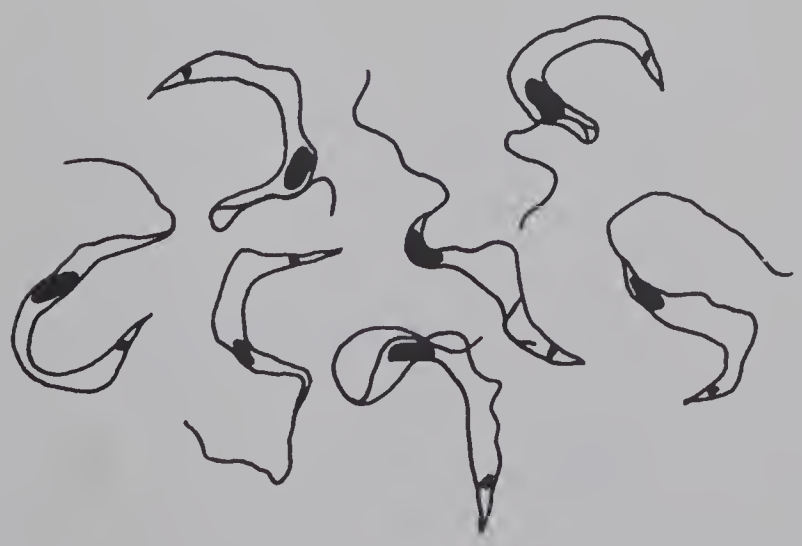
INCREASE



DECREASE



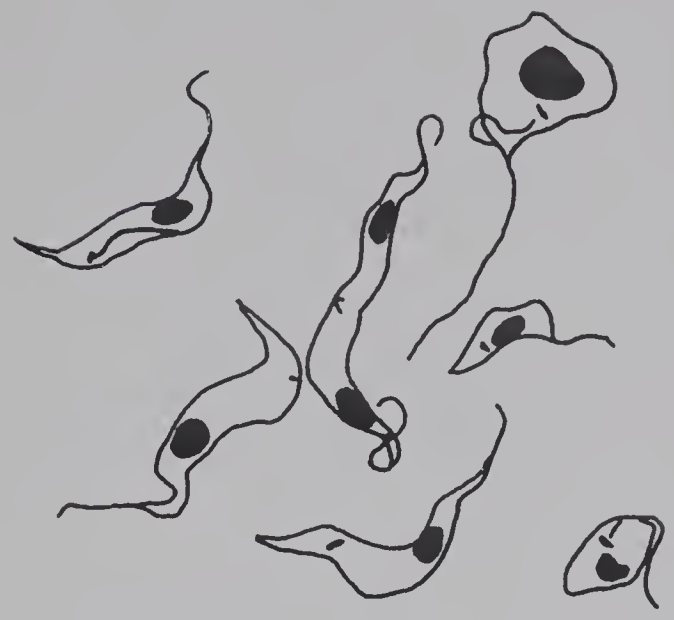
TERMINAL



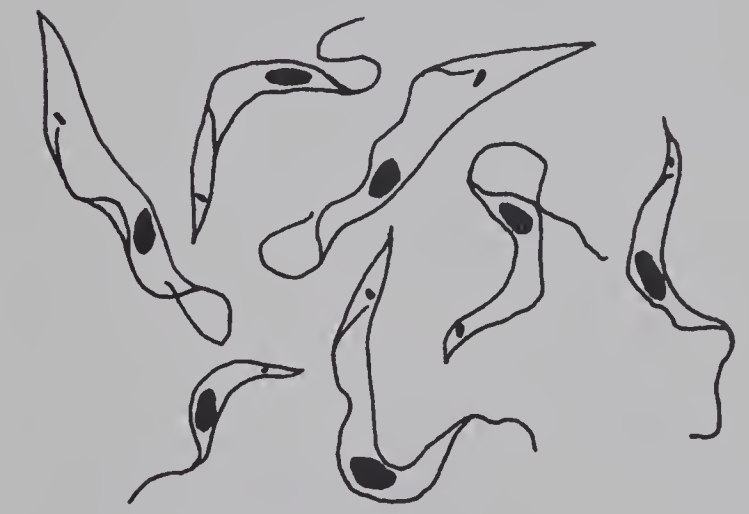
24 µm

Figure 19. Variations in T. lewisi morphology during the increase, decrease and terminal phases of infection in white rats.

INCREASE



DECREASE



TERMINAL

24 µm

Figure 20. Variations in T. musculi morphology during the increase and decrease phases of infection in white mice.

INCREASE

DECREASE

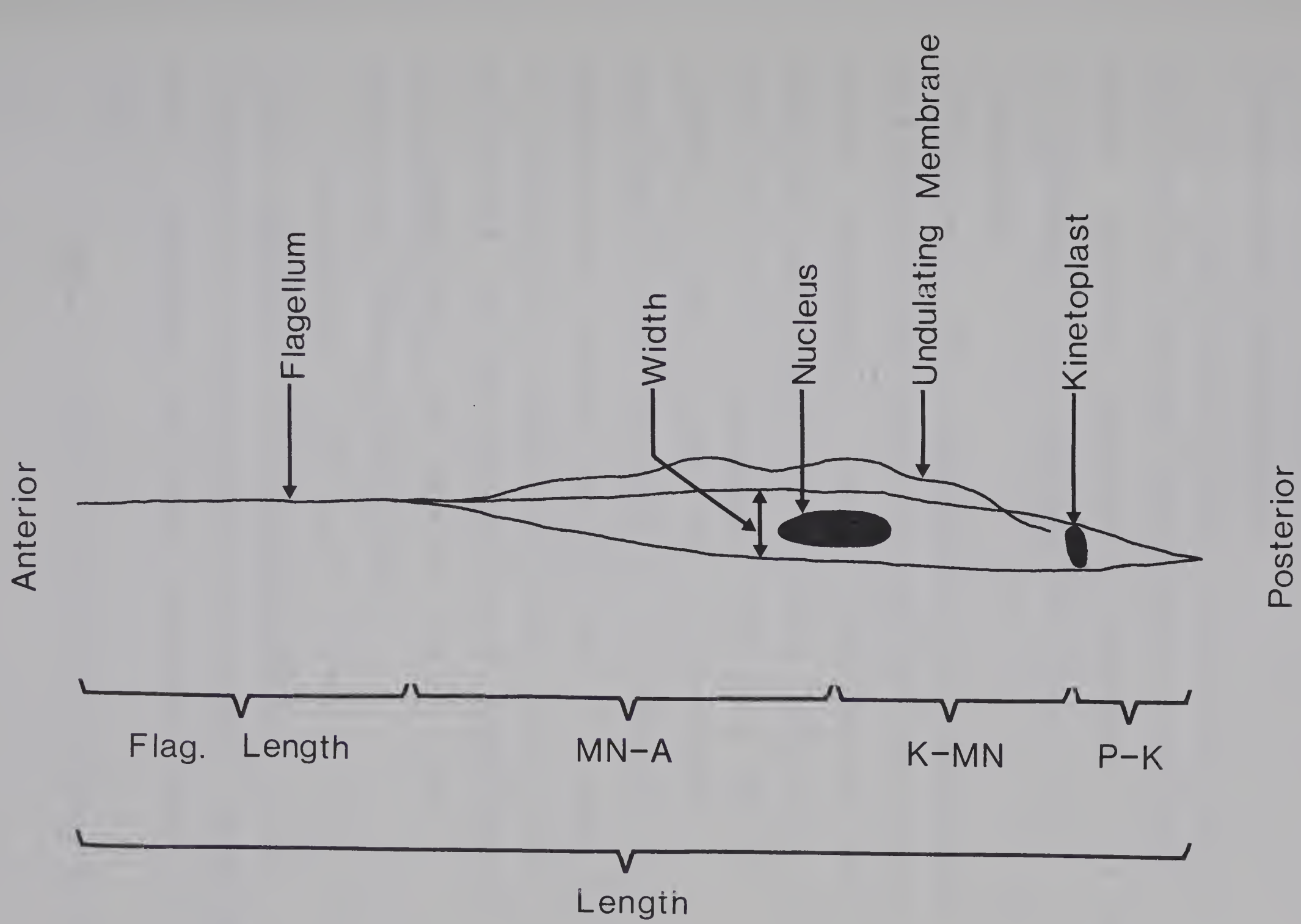
24 µm

Figure 21. Generalized drawing of a trypanosome to show major features and measurement regions.

P-K: posterior end of body to middle of kinetoplast

K-MN: middle of kinetoplast to middle of nucleus

MN-A: middle of nucleus to anterior end of body (not including flagellum)


Anterior
Flagellum
Width
Nucleus
Undulating Membrane
Kinetoplast
Posterior
Flag. Length
MN-A
K-MN
P-K
Length

DISCUSSION

Prevalence of Trypanosomiasis

It is questionable whether the prevalence data for 1971 (Table 1) should be interpreted as indicating a general increase in prevalence of trypanosomes. All the *S. columbianus* and *S. franklinii* and 75% of the *S. richardsonii* collected in 1971 were taken from only one locality each. The *S. columbianus* and *S. richardsonii* were collected from localities with very dense ground squirrel populations, a situation which may have facilitated more rapid transfer of infection. This same situation existed for *S. undulatus* collected in 1970 and probably accounts (in part) for the high (42.4%) prevalence of infection (Table 1). In addition, all *S. undulatus* were collected July 15th about two weeks after the susceptible (or recently infected) juvenile squirrels had emerged. Too few individuals of *S. franklinii* and *S. tridecemlineatus* were sampled in 1971 to give satisfactory indices of prevalence.

The trend for all three years, however, seems to be that *S. franklinii* and *S. tridecemlineatus* have low prevalences of infection (about 6%) whereas *S. columbianus* and *S. richardsonii* have higher prevalences, around 15% (Table 1).

As is shown in Table 2 trypanosomes are detected in

approximately twice as many ground squirrels if a more sensitive technique is used. Thus, the number of infected ground squirrels of each species in Table 1 probably represents about one-half the actual number. Similar results have been recorded by Bennett (1962) for birds from Ontario infected with trypanosomes and microfilariae.

Galuzo and Novinskaya (1968) examined thin blood smears from individuals of S. f. fulvus, S. p. pygmaeus and S. p. brevicauda collected from different localities in Russia over a six-year period and found that prevalences of infection fluctuated from year to year both within and between species. Prevalences varied from 0% (0/2 individuals of S. p. brevicauda) to 16.7% (1/6 individuals of both S. p. pygmaeus and S. p. brevicauda).

Fluctuations in prevalence of trypanosomes for individuals of two different genera of sciurids have also been recorded by Dorney (1969). Dorney attempted to determine (using stained thin blood smears) the natural fluctuations of two lewisi-like trypanosomes (not yet named, although Dorney determined them to be host specific) in Tamiasciurus hudsonicus (Erxleben) and Tamias striatus (L.) all collected at one location, Trout Lake, Wisconsin. Prevalences in the T. hudsonicus population were 4% (1/26) in 1961, 37% (19/52) in 1962 and 15% (11/73) in 1963.

Prevalences in the T. striatus population were 42% (34/80) in 1961, 25% (28/106) in 1962 and 12% (12/97) in 1963.

From these studies it would appear that yearly fluctuations in prevalence are common. However, Dorney's data were all collected at one location as were Galuzo and Novinskaya's for each host species within any one year (except for S. f. fulvus which was collected from three localities in 1954). Consequently, sampling ground squirrels from a large number of widespread localities (such as I did in 1969 and 1970) may give a more accurate indication of overall prevalence.

In contrast to fluctuations in prevalences between years those within any one year seem to show the same pattern, at least for S. richardsonii (Figure 5). The higher prevalences of infection recorded in April as opposed to May might represent a recrudescence of infection in individual ground squirrels brought about by the physiological changes that occur during emergence from hibernation. The infections shown in Figure 6 might support this hypothesis even though the slight increases in infection that occurred in 2/3 individuals following hibernation resemble the small fluctuations which occur in the terminal phase of experimental (Figures 7 to 11) and natural (Figure 13) infections. Although the data in Figure 6 are too limited to prove that there is no

recrudescence following hibernation, they do show that trypanosomes can survive (for at least four months) the physiological changes that take place in the ground squirrel's body during hibernation.

The peak prevalence in June may be due to the large number of susceptible young which have recently been weaned and have left their mothers' burrows to fend for themselves. This would increase their chances of coming into contact with other ground squirrels which are infected. In addition, many of the offspring from infected mothers might already be infected since they have been in contact with their mothers (and associated ectoparasites) for at least three weeks, a period in which there are undoubtedly many opportunities for natural transmission. Since parasitaemia may last one to two months in individuals of S. richardsonii (Figures 7, 11) young ground squirrels would still be infected when they emerged in June.

Natural Transmission of Trypanosomes

Hilton and Mahrt (1971) have shown that, of the ectoparasites present on three species of ground squirrels in Alberta, only fleas and lice could serve as efficient vectors since they are the only ectoparasites which are abundant and widely distributed on ground squirrels. Of these two groups fleas are the more likely vectors because (unlike lice) they are active and transfer readily

from individual to individual of a host species (Hopkins, 1949; 1957). In all cases studied, fleas have been the biological vectors of lewisi-like trypanosomes of rodents even though lice can be mechanical vectors (providing they contain infected undigested blood) if they are ingested by a susceptible host (Wenyon, 1926). It is only in fleas, however, in which trypanosomes can undergo cyclic developmental changes that result in infective forms being passed out with the feces. Transmission occurs when these infective feces are ingested or crushed into breaks in the host's skin. Fleas are therefore mechanical (in the same fashion as lice) and biological vectors. I have no data proving that fleas are vectors of the trypanosomes of ground squirrels.

Although I have been able to infect ground squirrels of different species with trypanosome strains from other species of ground squirrels, I do not know whether this transmission occurs in nature. Natural cross transmission did not appear to take place between individuals of S. richardsonii in area A and S. franklinii in area B (Figure 4) even though 22.2% of the S. richardsonii in area A were infected. It is possible that there was insufficient movement of ground squirrels between the two areas for the exchange of infected ectoparasites necessary to produce infection. Ectoparasite exchange

does occasionally occur between host species because fleas of the species Opisocrostis bruneri, normally specific for S. franklinii, have been recorded from S. richardsonii and S. tridecemlineatus (Holland, 1949). Such exchanges could easily occur if individuals of one species of ground squirrel enter the (abandoned or temporarily vacant) burrows of another. This would provide an opportunity for fleas (which are nest parasites) to transfer to a different host species.

In Alberta, the ranges of the following ground squirrels overlap: S. franklinii, S. richardsonii and S. tridecemlineatus; S. columbianus, S. richardsonii and S. tridecemlineatus; and S. columbianus and S. lateralis. Within these overlapping ranges I have often seen individuals of two or three species living within a few yards of one another. In these situations natural cross transmission might occur.

Host Specificity of Ground Squirrel Trypanosomes

White rats and white mice could not be infected with the trypanosome strain from naturally infected S. richardsonii. This corroborates the related findings of Becker and Roudabush (1934), Bozhenko (1927) Culbertson (1941), Davis (1952), Dorney (1967), Galuzo and Novinskaya (1968), Grewal (1957), Molyneux (1967a & b), Quay (1955), and Wood (1936), who all found it was impossible to infect

heterologous hosts (especially those from different genera and higher taxonomic categories).

As mentioned in the introduction, Bozhenko (1927) and Galuzo and Novinskaya (1968) successfully produced cross-infections between two or more species of Asian Spermophilus. In contrast, Becker and Roudabush (1934) were unable to infect S. tridecemlineatus with the trypanosome T. hixsoni (from S. franklinii), but later successfully infected the same individuals of S. tridecemlineatus with the trypanosome T. iowensis (from S. tridecemlineatus). None of the above authors gave any data on the number of ground squirrels of each species in which cross-infections were attempted.

In my cross transmission experiments (Table 3) the species of ground squirrel, and number of individuals of each species that could be successfully infected depended upon the trypanosome strain inoculated and the species of recipient squirrel. Thus, varying numbers of individuals of all six host species could be infected with the trypanosome strain from S. richardsonii, whereas only small numbers of individuals of 2/4 species of squirrels could be infected when the trypanosome strain from S. tridecemlineatus was used. It is likely that failure to infect more ground

squirrels with the trypanosome strain from S. columbianus was a result of immune hosts being used as recipients. This is suggested by the fact that of the 13 individuals which were unable to be infected the first time none could later be infected with the trypanosome strain from S. richardsonii. It is possible that some of these failures to produce experimental infections were due to incorrect inoculation sites, even though all injections were made intraperitoneally. Simmons, et al. (1963) have shown that during intraperitoneal inoculations of trypanosomes (species not specified) into mice the needle is, occasionally, inadvertently inserted into the stomach or intestinal lumen, sites where infections will not ensue.

There is a certain amount of host specificity involved in experimental ground squirrel infections which prevents cross transmission between some individuals of certain host species. Thus, 22/22 S. richardsonii and 9/9 S. tridecemlineatus individuals (all laboratory reared) were heavily infected with the S. richardsonii trypanosome strain whereas of the litter mates, only 16/22 S. richardsonii and 7/9 S. tridecemlineatus developed light infections when inoculated with the S. columbianus trypanosome strain. The six S. richardsonii individuals which failed to develop infections the first time (with the S. columbianus trypanosome strain) later became heavily infected when inoculated

with the strain from S. richardsonii.

Even though there are differences among trypanosome strains once a ground squirrel has lost its natural infection it cannot be reinfected with the same, or a different, strain of trypanosome (Table 4). In addition, I was unable to produce super-infections in ground squirrels using the same or different trypanosome strains. This suggests there are basic antigens common to all trypanosome strains and once ground squirrels develop antibodies to these antigens, reinfection cannot normally be effected. Similar results have been obtained with the T. brucei group of pathogenic African trypanosomes (Zuckerman and Ristic, 1968). In this species group there are both shared and variant-specific antigens.

Intensity and Duration of Parasitaemia in Experimental Infections

As has been shown in Figures 7 to 11, the course of an experimental infection is determined by both individual and species differences among hosts. Taking into consideration wide individual variability, ground squirrels of S. columbianus, S. franklinii, S. richardsonii and S. undulatus can be placed in one group since all have similar infections while those of S. lateralis and S. tridecemlineatus are different from one another as well as from the S. columbianus-S. franklinii-S. richardsonii-S.

undulatus group.

All the infections in ground squirrels are different from those produced in white rats and white mice by the trypanosomes T. lewisi and T. musculi, respectively (Figure 12). This emphasizes that the host species (and also trypanosome species) determines the intensity and duration of experimental trypanosome infections.

Following termination of parasitaemia in ground squirrels it appears that the immunity which has developed is sterile (i.e. trypanosomes are no longer present in the host's body) and of very long duration, possibly a life time (Table 4). Splenectomy did not result in recrudescence of infections. This is similar to immunity in white rats against the trypanosome, T. lewisi (Corradetti, 1963).

Size Comparisons of Trypanosome Strains

Host individuals exert an effect upon trypanosome size (Figures 16, 17). If allowances are made for this variation the five trypanosome strains obtained from naturally infected ground squirrels can be divided into two groups. The strains from S. columbianus, S. richardsonii and S. undulatus form one group while those from S. franklinii and S. tridecemlineatus comprise the second group.

The differences in trypanosome size between natural and experimental infections are probably not the result of

experimental infections being initiated with the trypanosome strain from S. richardsonii. Even within this host species, trypanosomes from the natural and experimental infections are significantly different in size (Table 9b). One reason for these size differences may be that cyclical development is required in the arthropod vector(s) before the strain sizes shown in Table 5 can be attained. It has been shown for the T. brucei group of pathogenic African trypanosomes that cyclical development in the tsetse fly vector is required to return the relapse strains (which differ antigenically from one another) to the antigenic type of the parent strain (Brown, 1963; Weinman, 1968). Although this latter evidence does not demonstrate size differences, it does indicate cyclical development in the vector is necessary to stabilize modifying influences exerted by the vertebrate host.

A strong influence is exerted on trypanosome size by the host species. Thus, if different individuals of S. columbianus and S. tridecemlineatus are inoculated with the S. columbianus, S. richardsonii and S. tridecemlineatus trypanosome strains (Table 7) and S. columbianus and S. richardsonii strains (Table 8), respectively almost all experimental infections produced in either one of these two host species will not differ in size. Conversely, if equal portions of the same inoculum are

injected into individuals of S. tridecemlineatus and ground squirrels of another species the size differences between trypanosomes from the two infections that are produced will often be significantly different (Tables 12, 16).

Body measurements with a high coefficient of variation (C.V.) during the increase phase of a trypanosome infection are an indication of trypanosome reproduction in the host's bloodstream. This has been shown for infections of the trypanosome T. lewisi in white rats Taliaferro, 1923; Taliaferro and Taliaferro, 1922). Demonstration of reproducing forms in blood smears (Figure 19) is confirmation that such reproduction occurs. The decrease and terminal phases of infection have lower C.V. values due to the removal of all young dividing (and therefore variable) trypanosomes by the first-crisis antibody, leaving the monomorphic "adult" forms (Ormerod, 1963; Taliaferro, 1923; Taliaferro and Taliaferro, 1922). My data (Table 17g) show that the decrease phase has the highest C.V. followed in turn by the increase and terminal phases. This difference may be due to strain differences since the L strain of T. lewisi (which I used) produced experimental infections considerably different from those produced by Taliaferro's strain of T. lewisi.

A similar type of reproduction occurs in T. musculi trypanosome infections in white mice except that differences in C.V. are not as great (D'Alesandro, 1970). My data (Figure 20, Table 17h) agree.

Trypanosomes of ground squirrels do not have a reproductive stage in the bloodstream. This was determined by the similar coefficients of variation within each measurement region (Table 17a to f) and by the monomorphic trypanosomes present in all three infection phases (Figure 18). This means there must be a tissue stage of reproduction from which trypomastigotes are released into the bloodstream following a prepatent period of six to seven days (as determined by hemocytometer counts). Reproduction of this type has been found to occur in the rodent trypanosomes T. evotomys, T. microti, T. nabiasi, and T. zapi (Molyneux, 1970).

The body measurements I determined for trypanosomes from naturally infected ground squirrels are considerably larger than those recorded by other investigators (although my measurements show similar differences between strains). Thus, Becker and Roudabush (1934) found total length of the trypanosomes, T. hixsoni (from S. franklinii) and T. iowensis (from S. tridecemlineatus) to be 32.0 and 26.3 µm, respectively. In contrast, my data for the strains from these two host species are 39.5 and 38.8 µm, respec-

tively. Watson and Hadwen (1912) only measured a few (exact numbers not stated) trypanosomes of T. citelli from S. richardsonii and recorded the mean length as 35.0 µm. This compares with a mean length of 47.6 µm which I obtained for trypanosomes from the same host species. Since trypanosomes from S. columbianus and S. undulatus (in North America) have not previously been reported, no comparative data are available. Davis (1952) and Noble and Shipman (1958) recorded total length for two different populations of T. otospermophili from S. beecheyi as 30.7 and 25.2 µm, respectively. Galuzo and Novinskaya (1968) do not give measurements for the populations of trypanosomes they described. However, Bozhenko (1927) determined mean total length for trypanosomes from S. f. fulvus, S. pygmaeus mugozaricus and S. p. musicus to be 32.5, 32.4 and 33.0 µm, respectively.

Similar size differences occurred between the measurements I obtained for the T. lewisi and T. musculi strains and those determined for different strains of the same two species by Taliaferro (1923).

Most of the above authors do not state what measuring devices they used but in the past it has usually been calipers or a series of short straight lines drawn along the central axis of the trypanosome. Since I used a calibrated map measurer I was able to follow every curve in the

trypanosome's body and my measurements would be greater than could be obtained with either calipers or straight lines.

Size discrepancies may also be due to differences in: optical equipment, fixing and staining methods, as well as strain variability. Fixing, staining, and different strains have been shown to produce size differences with T. lewisi (Taliaferro, 1923).

TAXONOMIC STATUS OF GROUND SQUIRREL TRYPANOSOMES

Although the trypanosomes of ground squirrels are not distinguishable from T. lewisi and T. musculi by size alone (Table 6) they can be separated because the latter have 1) variable body size during the increase stage of infection, 2) a different type of reproduction in the vertebrate host, 3) rigid host specificity, and 4) large differences in duration and intensity of infections. These characters taken together serve to define T. lewisi and T. musculi as distinct species readily separable from the trypanosomes of ground squirrels.

Since the trypanosome strains (so far examined) from ground squirrels are all morphologically identical they cannot be separated into different species on the basis of morphological criteria. There are differences between strains as regards mensural variations, intensity and duration of infections, host specificity, and geographical restriction. However, these are all characters which, when taken separately or in combination, could (at the most) be used only in distinguishing subspecies, not species (Corliss, 1962; Hoare, 1966; Sonneborn, 1957).

The trypanosome strains from different species of ground squirrels should not be designated as subspecies because 1) ground squirrel trypanosomes are not important enough (from a medical standpoint) to warrant sepa-

ration into subspecies as has been done for those of the T. brucei group (Hoare, 1966), 2) strain differences seem to be host influenced, and 3) geographical isolation of S. undulatus from all other North American ground squirrels has not resulted in appreciable differences between the trypanosome strain in S. undulatus and those in the other host species. The fact that strain differences are host influenced is further emphasized by noting that trypanosome strains from ground squirrels of the subgenus Spermophilus (i.e. S. columbianus, S. richardsonii and S. undulatus) are all similar to one another (as regards size, types of infection and host specificity), but different from the strains found in S. (Poliocitellus) franklinii and S. (Ictidomys) tridecemlineatus. Trypanosome strains from ground squirrels of the latter subgenera show some differences from each other (size in experimental infections, levels of host specificity, duration of infections) as well as some similarities (size in natural infections, intensity of infections).

Hoare's (1966, 1967) suggested application of the term xenodeme to host-restricted trypanosome populations does not really apply to trypanosome strains from ground squirrels since in these latter cases host specificity is not absolute. In addition, geographical ranges of many ground squirrels overlap (Hall and Kelson, 1959)

and it has been shown (Holland, 1949) that exchanges of fleas can occur among ground squirrels of different species, thus perhaps providing opportunities for natural cross transmission (assuming fleas are vectors). Gilmour and Heslop-Harrison's (1955) term plastodeme is partially applicable to trypanosome strains from ground squirrels since it denotes populations differing phenotypically. However, even plastodeme is not entirely satisfactory because it only indicates there are differences without specifying what types.

As most of the differences among trypanosome strains of ground squirrels are host influenced, it would be advantageous to have a collective term which denotes this variation. Consequently, I believe it is useful to use two descriptive prefixes in front of the root (deme) as has been done by Gilmour and Heslop-Harrison (1955). Thus, populations of trypanosomes from different species of ground squirrels would be termed plastoxenodemes, i.e. populations whose differences are host-influenced. Terminology of this type, perhaps objectionable from the standpoint of phonetics, is a good means for describing the type of variation present among populations.

Since most differences among trypanosome strains of ground squirrels result from host influences (and host specificity is not absolute) there is no basis for preserving the specific status of T. citelli, T. hixsoni

and T. iowensis (described from S. richardsonii, S. franklinii and S. tridecemlineatus, respectively). Although I have no comparable information for the trypanosome strain (described as T. otospermophili) from S. beecheyi in California, there are at least four reasons for believing that it is also a plastoxenodeme. 1) S. beecheyi is not geographically isolated and has overlapping distributions with S. beldingi Merriam, S. lateralis and S. mohavensis Merriam. These latter three species also have overlapping distributions with one or more other North American ground squirrels, thus providing a continuum with the five species of ground squirrels I worked with in Alberta. This would (in theory, at least) provide opportunities for natural cross transmission. 2) Even though S. undulatus in North America is geographically isolated from all other North American species, the trypanosomes present in S. undulatus are very similar to those from S. columbianus and S. richardsonii as regards size and types of infection produced (experimentally). In contrast, the S. franklinii and S. tridecemlineatus trypanosome strains are different (in ways previously described) from one another as well as from the S. columbianus and S. richardsonii strains, even though one or more of the host species have overlapping ranges. 3) Similarly to my work, Bozhenko (1927) and Galuzo and Novinskaya (1968) deter-

mined (on the basis of complete cross transmission) that there is only one species of trypanosome (T. spermophili) present in Eurasian ground squirrels. 4) Trypanosomes from S. beecheyi are identical in morphology to all other ground squirrel trypanosomes as well as being similar in size to the plastoxenodemes from S. franklinii and S. tridecemlineatus.

As a result of the foregoing I believe there is strong evidence to suggest that only one species of trypanosome (T. otospermophili) is present in ground squirrels of the genus Spermophilus in North America. It is probable that T. otospermophili and T. spermophili are the same species based on my work, the cross transmission experiments of Bozhenko (1927) and Galuzo and Novinskaya (1968), and the fact that S. undulatus has a Holarctic distribution which overlaps with the distributions of other species of ground squirrels in south-central Asia. However, until more conclusive evidence is obtained the two species should remain separate.

A revised description of T. otospermophili (using mensural data from the literature as well as my own), its synonyms and recorded hosts are given below.

Trypanosoma (Herpetosoma) otospermophili (Wellman and Wherry, 1910) Laveran, 1911

SYNONYMS: Trypanosoma citelli Watson and Hadwen, 1912;

T. hixsoni Becker and Roudabush, 1934; T. iowensis Becker and Roudabush, 1934.

DESCRIPTION: Characters as for the genus, in addition to being lewisi-like (i.e. resembling the trypomastigote stage of T. lewisi) in general appearance; body measurements very variable depending upon host sex and species. Total length 25.2-55.0 µm (mean 39.4 µm); width at widest point (not including undulating membrane) 1.5-4.0 µm (mean 2.4 µm); posterior end of body to kinetoplast 1.5-7.5 µm (mean 3.9 µm); kinetoplast to middle of nucleus 8.3-21.0 µm (mean 13.4 µm); middle of nucleus to anterior end of body 6.0-21.0 µm (mean 10.9 µm); length of free flagellum 6.0-24.0 µm (mean 11.1 µm); nucleus length 2.4-6.0 µm (mean 3.2 µm). Kinetoplast round to triangular, occupying entire body width; nucleus elongate ovoid with long axis oriented parallel to body length, not usually occupying entire body width. Kinetoplast and nucleus stain medium to deep purple with Giemsa or Wright's blood stains while body cytoplasm stains pale blue or pale violet.

RECORDED HOSTS: Spermophilus beecheyi, S. columbianus, S. franklinii, S. richardsonii, S. tridecemlineatus, S. undulatus plesius. In addition, S. lateralis has been experimentally infected.

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APPENDIX

SIZE COMPARISONS OF TRYPANOSOMES

Table 5. Comparison of trypanosome size (in mμ†) among the five species of naturally infected ground squirrels.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant* sets 1	Non-significant* sets 2
Length (L)	T	3	15	38.8	1.8	0.5	5	34.5	42.0		
	F	3	24	39.5	2.4	0.5	6	32.5	43.0		
	U	12	62	47.1	3.9	0.5	8	34.5	54.0		
	C	8	69	47.2	2.7	0.3	6	36.0	54.0		
	R	37	117	47.6	2.7	0.3	6	39.0	55.0		
Width (W)	F	3	24	2.2	0.6	0.1	27	1.5	3.0		
	C	8	69	2.5	0.5	0.1	21	1.5	4.0		
	T	3	15	2.6	0.4	0.1	16	1.5	3.0		
	R	37	117	2.6	0.5	0.1	19	1.5	4.0		
	U	12	62	2.7	0.5	0.1	18	2.0	4.0		
P-K	F	3	24	3.4	1.0	0.2	29	1.5	5.0		
	T	3	15	3.4	0.5	0.1	15	3.0	4.5		
	R	37	117	4.5	1.0	0.1	22	3.0	7.5		
	C	8	69	5.0	0.8	0.1	16	3.0	7.0		
	U	12	62	5.5	1.1	0.1	20	3.0	7.5		
K-MN	T	3	15	13.5	1.3	0.3	10	12.0	16.0		
	F	3	24	13.6	2.0	0.4	15	10.0	17.0		
	U	12	62	15.9	1.4	0.2	9	11.0	18.0		
	C	8	69	16.5	1.3	0.2	8	14.0	21.0		
	R	37	117	16.6	1.3	0.1	8	13.0	19.5		

Table 5. (continued)

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant* sets 1	Non-significant* sets 2
MN-A	F	3	24	10.9	1.6	0.3	15	8.0	13.5	|	
	U	12	62	11.3	2.2	0.3	19	7.0	16.0	|	
	T	3	15	11.6	1.8	0.5	16	9.0	16.0	|	|
	C	8	69	12.4	2.1	0.3	17	7.0	18.0	|	|
	R	37	117	12.7	2.4	0.2	19	6.0	21.0		|
Nucleus (N)	T	3	15	3.4	0.4	0.1	12	3.0	4.0	|	
	U	12	62	3.4	0.9	0.1	25	3.0	6.0	|	
	F	3	24	3.5	0.6	0.1	17	3.0	4.5	|	
	C	8	69	3.7	0.7	0.1	19	3.0	6.0	|	
	R	37	117	3.8	0.8	0.1	21	3.0	6.0	|	
Flagellum (F)	T	3	15	10.3	2.3	0.6	22	7.0	17.0		|
	F	3	24	11.7	2.5	0.5	21	8.0	16.5		|
	C	8	69	13.3	2.0	0.2	15	8.0	18.0	|	
	R	37	117	13.8	2.8	0.3	20	6.0	24.0	|	
	U	12	62	14.4	3.1	0.4	21	8.0	19.5	|	

*P = 0.01 for Tables 5 to 17; means not significantly different are joined by a vertical line.

Note: NH: number of hosts; NT: number of trypanosomes; S.D.: standard deviation; S.E.: estimated standard error; C.V.: coefficient of variation expressed in percent.

†Should be µm for this and all following tables.

Table 6. Comparison of trypanosome size (in mμ) among all species of ground squirrels (experimentally infected with the trypanosome strain from S. richardsonii), white rats (infected with T. lewisi), and white mice (infected with T. musculi).

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	2	3	4
Length	T	3	67	39.3	2.4	0.3	6	32.5	44.5				
	X	3	100	40.3	4.4	0.4	11	22.5	51.0				
	M	10	146	41.9	4.2	0.4	10	30.0	51.0				
	L	5	160	43.0	3.2	0.3	7	31.5	50.0				
	F	3	66	44.0	2.5	0.3	6	37.0	48.0				
	U	2	81	45.0	2.3	0.3	5	37.5	50.0				
	C	8	83	45.0	3.0	0.3	7	37.0	52.0				
	R	9	227	45.4	2.6	0.2	6	35.0	51.0				
Width	L	5	160	2.2	0.5	0.0	24	1.5	3.0				
	F	3	66	2.5	0.5	0.1	21	1.5	3.0				
	C	8	83	2.5	0.5	0.1	21	1.5	3.0				
	T	3	67	2.6	0.5	0.1	19	1.5	3.0				
	U	2	81	2.7	0.5	0.1	18	2.0	4.0				
	R	9	227	2.7	0.5	0.0	18	1.5	3.0				
	X	3	100	3.2	0.7	0.1	23	2.0	6.0				
	M	10	146	3.6	0.8	0.1	23	2.0	6.0				
P-K	T	3	67	3.6	0.9	0.1	25	2.0	6.0				
	F	3	66	3.8	0.7	0.1	19	2.0	6.0				
	U	2	81	3.8	0.8	0.1	20	2.0	6.0				
	R	9	227	3.9	0.8	0.1	21	2.0	6.0				
	L	5	160	4.0	0.8	0.1	20	2.0	6.0				
	C	8	83	4.0	0.9	0.1	22	2.0	7.0				
	X	3	100	4.6	1.8	0.2	40	2.0	12.0				
	M	10	146	8.0	2.5	0.2	32	3.0	13.0				

Table 6. (continued)

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	2	3	4
K-MN	M	10	146	10.2	1.5	0.1	15	6.0	13.5				
	T	3	67	13.8	1.3	0.2	9	12.0	16.0				
	X	3	100	15.0	1.8	0.2	12	7.5	19.5				
	F	3	66	15.1	1.4	0.2	9	12.0	19.5				
	L	5	160	15.3	1.5	0.1	9	12.0	19.0				
	U	2	81	15.5	1.5	0.2	10	10.0	19.0				
	C	8	83	15.6	1.6	0.2	10	12.0	19.0				
	R	9	227	16.2	1.3	0.1	8	12.0	20.0				
MN-A	T	3	67	9.3	1.8	0.2	19	5.0	13.5				
	X	3	100	9.4	1.9	0.2	20	3.0	13.5				
	L	5	160	10.1	2.4	0.2	24	4.0	16.0				
	F	3	66	10.6	1.9	0.2	18	6.0	15.0				
	U	2	81	10.9	1.9	0.2	17	6.0	15.0				
	C	8	83	11.2	1.9	0.2	16	7.0	16.5				
	R	9	227	11.4	2.2	0.1	19	4.5	18.0				
	M	10	146	13.6	2.4	0.2	18	8.0	19.5				
Nucleus	C	8	83	3.6	0.7	0.1	18	2.0	5.0				
	X	3	100	3.7	0.7	0.1	19	2.0	5.0				
	F	3	66	3.9	0.7	0.1	19	3.0	6.0				
	M	10	146	4.1	0.6	0.1	15	3.0	6.0				
	U	2	81	4.1	0.7	0.1	17	3.0	6.0				
	T	3	67	4.4	1.0	0.1	24	3.0	6.0				
	L	5	160	4.4	0.8	0.1	19	2.0	7.0				
	R	9	227	4.5	0.9	0.1	19	3.0	7.0				

Table 6. (continued)

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	2	3	4
Flagellum	M	10	146	10.1	2.3	0.2	23	4.0	17.0				
	X	3	100	11.4	2.4	0.2	21	6.0	22.0				
	T	3	67	12.7	2.3	0.3	18	7.0	18.0				
	L	5	160	13.7	2.7	0.2	19	6.0	20.0				
	R	9	227	14.0	2.4	0.2	17	7.0	24.0				
	C	8	83	14.2	2.5	0.3	18	6.0	19.5				
	F	3	66	14.6	2.5	0.3	17	7.5	19.0				
	U	2	81	14.8	2.5	0.3	17	7.5	20.0				

Note: M: white mice; X: white rats.

Table 7. Comparison of trypanosome size (in mμ) among all natural and experimental (induced by trypanosome strains from three different species of ground squirrels) infections in S. columbianus.

Measurement	Trypanosome strain	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	Non-significant sets 2
Length	C → C	1	47	43.8	4.0	0.6	9	33.5	50.0		
	R → C	8	83	45.0	3.0	0.3	7	37.0	52.0		
	T → C	1	4	45.8	2.4	1.4	5	43.5	49.5		
	Nat.C	8	69	47.2	2.7	0.3	6	36.0	54.0		
Width	Nat.C	8	69	2.5	0.5	0.1	21	1.5	4.0		
	R → C	8	83	2.5	0.5	0.1	21	1.5	3.0		
	C → C	1	47	2.5	0.5	0.1	20	1.5	3.0		
	T → C	1	4	2.5	0.5	0.3	20	2.0	3.0		
P-K	R → C	8	83	4.0	0.9	0.1	22	3.0	7.0		
	T → C	1	4	4.5	0.9	0.5	20	4.0	6.0		
	C → C	1	47	4.6	0.9	0.1	20	3.0	6.0		
	Nat.C	8	69	5.0	0.8	0.1	16	3.0	7.0		
K-MN	C → C	1	47	15.2	1.8	0.3	12	10.5	18.0		
	R → C	8	83	15.6	1.6	0.2	10	12.0	19.0		
	T → C	1	4	16.1	1.2	0.7	7	15.0	18.0		
	Nat.C	8	69	16.5	1.3	0.2	8	14.0	21.0		
MN-A	R → C	8	83	11.2	1.9	0.2	16	7.0	16.5		
	C → C	1	47	11.6	2.4	0.4	21	7.5	16.0		
	T → C	1	4	12.3	2.1	1.2	17	10.0	15.0		
	Nat.C	8	69	12.4	2.1	0.3	17	7.0	18.0		

Table 7. (continued)

Measurement	Trypanosome strain	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	Non-significant sets 2
Nucleus	R → C	8	83	3.6	0.7	0.1	18	2.0	5.0		
	Nat.C	8	69	3.7	0.7	0.1	19	3.0	6.0		
	T → C	1	4	3.8	0.8	0.5	21	3.0	5.0		
	C → C	1	47	4.0	0.7	0.1	18	3.0	6.0		
Flagellum	C → C	1	47	12.6	2.7	0.4	21	6.0	19.5		
	T → C	1	4	12.9	1.5	0.9	12	11.0	15.0		
	Nat.C	8	69	13.3	2.0	0.2	15	8.0	18.0		
	R → C	8	83	14.2	2.5	0.3	18	6.0	19.5		

Note: Nat.C: naturally infected S. columbianus (C).
R → C: S. columbianus experimentally infected with strain from S. richardsonii (R).
C → C: S. columbianus experimentally infected with strain from S. columbianus.
T → C: S. columbianus experimentally infected with strain from S. tridecemlineatus (T).

Table 8. Comparison of trypanosome size (in mμ) among all natural and experimental (induced by trypanosome strains from two different species of ground squirrels) infections in S. tridecemlineatus.

Measurement	Trypanosome strain	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	Non-significant sets 2
Length	Nat.T	3	15	38.8	1.8	0.5	5	34.5	42.0		
	R → T	3	67	39.3	2.4	0.3	6	32.5	44.5		
	C → T	1	21	40.4	2.5	0.6	6	33.5	44.5		
Width	C → T	1	21	2.3	0.6	0.1	26	1.5	3.0		
	Nat.T	3	15	2.6	0.4	0.1	16	1.5	3.0		
	R → T	3	67	2.6	0.5	0.1	19	1.5	3.0		
P-K	Nat.T	3	15	3.4	0.5	0.1	15	3.0	4.5		
	R → T	3	67	3.6	0.9	0.1	25	2.0	6.0		
	C → T	1	21	3.6	0.9	0.2	25	2.0	6.0		
K-MN	Nat.T	3	15	13.5	1.3	0.3	10	12.0	16.0		
	C → T	1	21	13.6	1.4	0.3	10	10.5	16.0		
	R → T	3	67	13.8	1.3	0.2	9	12.0	16.0		
MN-A	R → T	3	67	9.3	1.8	0.2	19	5.0	13.5		
	C → T	1	21	10.3	1.4	0.3	14	7.0	13.0		
	Nat.T	3	15	11.6	1.8	0.5	16	9.0	16.0		
Nucleus	Nat.T	3	15	3.4	0.4	0.1	12	3.0	4.0		
	C → T	1	21	3.7	0.6	0.1	16	3.0	4.5		
	R → T	3	67	4.4	1.0	0.1	24	3.0	6.0		

Table 8. (Continued)

Measurement	Trypanosome strain	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	Non-significant sets 2
Flagellum	Nat.T	3	15	10.3	2.3	0.6	22	7.0	17.0		
	R → T	3	67	12.7	2.3	0.3	18	7.0	18.0		
	C → T	1	21	13.0	2.0	0.4	15	9.0	16.5		

Note: Nat.T: naturally infected S. tridecemlineatus (T).
C → T: S. tridecemlineatus experimentally infected with strain from S. columbianus (C).
R → T: S. tridecemlineatus experimentally infected with strain from S. richardsonii (R).

Table 9a. Comparison of trypanosome size (in mμ) between naturally and experimentally (induced with trypanosome strain from S. richardsonii) infected S. franklinii.

Measurement	Type of infection	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Nat.	3	24	39.5	2.4	0.5	6	32.5	43.0	
	Exp.	3	66	44.0	2.6	0.3	6	37.0	48.0	
Width	Nat.	3	24	2.2	0.6	0.1	27	1.5	3.0	
	Exp.	3	66	2.5	0.5	0.1	21	1.5	3.0	
P-K	Nat.	3	24	3.4	1.0	0.2	29	1.5	5.0	
	Exp.	3	66	3.8	0.7	0.1	18	2.0	6.0	
K-MN	Nat.	3	24	13.6	2.0	0.4	15	10.0	17.0	
	Exp.	3	66	15.1	1.4	0.2	9	12.0	19.5	
MN-A	Exp.	3	66	10.6	1.9	0.2	18	6.0	15.0	
	Nat.	3	24	10.9	1.6	0.3	15	8.0	13.0	
Nucleus	Nat.	3	24	3.5	0.6	0.1	17	3.0	4.5	
	Exp.	3	66	3.9	0.7	0.1	19	3.0	6.0	
Flagellum	Nat.	3	24	11.7	2.5	0.5	21	8.0	16.5	
	Exp.	3	66	14.6	2.5	0.3	17	7.5	19.0	

Table 9b. Comparison of trypanosome size (in mμ) between naturally and experimentally (induced with trypanosome strain from S. richardsonii) infected S. richardsonii.

Measurement	Type of infection	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Exp.	9	227	45.4	2.6	0.2	6	35.0	51.0	
	Nat.	37	117	47.6	2.7	0.3	6	39.0	55.0	
Width	Nat.	37	117	2.6	0.5	0.1	19	1.5	3.0	I
	Exp.	9	227	2.7	0.5	0.0	18	1.5	3.0	
P-K	Exp.	9	227	3.9	0.8	0.1	21	1.5	6.0	
	Nat.	37	117	4.5	1.0	0.1	22	3.0	7.5	
K-MN	Exp.	9	227	16.2	1.3	0.1	8	12.0	20.0	
	Nat.	37	117	16.6	1.3	0.1	8	13.0	19.5	
MN-A	Exp.	9	227	11.4	2.2	0.2	19	4.5	18.0	
	Nat.	37	117	12.7	2.4	0.2	19	6.0	21.0	
Nucleus	Nat.	37	117	3.8	0.8	0.1	21	3.0	6.0	
	Exp.	9	227	4.5	0.9	0.1	19	3.0	7.0	
Flagellum	Nat.	37	117	13.8	2.8	0.3	20	6.0	24.0	I
	Exp.	9	227	13.9	2.4	0.2	17	7.0	24.0	

Table 9c. Comparison of trypanosome size (in mμ) between naturally and experimentally (induced with trypanosome strain from S. richardsonii) infected S. undulatus.

Measurement	Type of infection	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Exp.	2	81	45.0	2.3	0.3	5	37.5	50.0	
	Nat.	12	62	47.1	3.9	0.5	8	34.5	54.0	
Width	Exp.	2	81	2.7	0.5	0.1	18	2.0	4.0	
	Nat.	12	62	2.7	0.5	0.1	18	2.0	4.0	
P-K	Exp.	2	81	3.8	0.7	0.1	20	2.0	6.0	
	Nat.	12	62	5.5	1.0	0.1	20	3.0	7.5	
K-MN	Exp.	2	81	15.5	1.5	0.2	10	10.0	19.0	
	Nat.	12	62	15.9	1.4	0.2	9	11.0	18.0	
MN-A	Exp.	2	81	10.9	1.9	0.2	17	6.0	15.0	
	Nat.	12	62	11.3	2.2	0.3	19	7.0	16.0	
Nucleus	Nat.	12	62	3.4	0.9	0.1	25	3.0	6.0	
	Exp.	2	81	4.1	0.7	0.1	17	3.0	6.0	
Flagellum	Nat.	12	62	14.4	3.1	0.4	21	8.0	19.5	
	Exp.	2	81	14.8	2.5	0.3	17	7.5	20.0	

Table 10a. Comparison of trypanosome size (in mμ) between naturally infected males and females of S. columbianus.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	4	23	46.2	3.0	0.6	6	36.0	50.0	
	♀	4	46	47.7	2.4	0.4	5	42.5	54.0	
Width	♀	4	46	2.4	0.5	0.1	21	1.5	3.0	
	♂	4	23	2.6	0.6	0.1	23	1.5	4.0	
P-K	♂	4	23	5.0	0.8	0.2	16	3.0	6.0	
	♀	4	46	5.0	1.0	0.1	20	3.0	7.0	
K-MN	♂	4	23	16.4	1.0	0.2	6	15.0	18.0	
	♀	4	46	16.6	1.5	0.2	9	14.0	21.0	
MN-A	♂	4	23	12.3	2.6	0.6	21	7.0	18.0	
	♀	4	46	12.4	1.9	0.3	15	9.0	18.0	
Nucleus	♂	4	23	3.6	0.7	0.2	19	3.0	5.0	
	♀	4	46	3.7	0.8	0.1	22	3.0	6.0	
Flagellum	♂	4	23	12.5	2.0	0.4	16	8.0	16.0	
	♀	4	46	13.7	2.0	0.3	15	9.0	18.0	

Table 10b. Comparison of trypanosome size (in mμ) between naturally infected males and females of S. franklinii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	1	10	38.1	2.4	0.8	6	32.5	40.5	
	♀	2	14	40.6	1.7	0.5	4	38.0	43.0	
Width	♀	2	14	2.1	0.5	0.1	24	1.5	3.0	
	♂	1	10	2.4	0.5	0.2	21	2.0	3.0	
P-K	♂	1	10	2.6	0.6	0.2	23	1.5	3.0	
	♀	2	14	3.9	0.8	0.2	21	3.0	5.0	
K-MN	♂	1	10	12.1	1.3	0.4	11	10.0	13.5	
	♀	2	14	14.7	1.5	0.4	10	12.0	17.0	
MN-A	♀	2	14	10.4	1.6	0.4	15	8.0	13.0	
	♂	1	10	11.7	1.3	0.4	11	9.0	13.5	
Nucleus	♀	2	14	3.5	0.5	0.1	14	3.0	4.0	
	♂	1	10	3.6	0.6	0.2	17	3.0	4.5	
Flagellum	♀	2	14	11.5	2.8	0.8	24	8.0	16.5	
	♂	1	10	11.9	1.9	0.6	16	9.0	15.0	

Table 10c. Comparison of trypanosome size (in mμ) between naturally infected males and females of S. richardsonii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	12	29	46.3	2.3	0.4	5	39.0	50.0	
	♀	25	88	48.0	2.6	0.3	5	39.0	55.0	
Width	♀	25	88	2.6	0.5	0.0	19	1.5	3.0	
	♂	12	29	2.7	0.5	0.1	19	2.0	4.0	
P-K	♂	12	29	4.4	1.0	0.2	23	3.0	6.0	
	♀	25	88	4.5	1.0	0.1	22	3.0	7.5	
K-MN	♂	12	29	16.3	1.5	0.3	9	13.0	19.5	
	♀	25	88	16.7	1.2	0.1	7	13.5	19.5	
MN-A	♂	12	29	12.5	2.2	0.4	18	6.0	16.0	
	♀	25	88	12.7	2.4	0.3	19	6.0	21.0	
Nucleus	♂	12	29	3.7	0.8	0.2	22	3.0	6.0	
	♀	25	88	3.8	0.8	0.1	21	3.0	6.0	
Flagellum	♂	12	29	13.0	2.7	0.5	21	6.0	18.0	
	♀	25	88	14.1	2.8	0.3	20	6.0	24.0	

Table 10d. Comparison of trypanosome size (in mμ) between naturally infected males and females of S. undulatus.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	6	19	46.7	5.0	1.1	11	34.5	54.0	
	♀	6	43	47.2	3.4	0.5	7	39.0	53.0	
Width	♀	6	43	2.7	0.5	0.1	17	2.0	3.0	
	♂	6	19	2.7	0.6	0.1	21	2.0	4.0	
P-K	♂	6	19	5.2	1.1	0.3	22	3.0	7.5	
	♀	6	43	5.7	1.1	0.2	19	3.0	7.0	
K-MN	♀	6	43	15.7	1.3	0.2	8	13.5	18.0	
	♂	6	19	16.2	1.6	0.4	10	11.0	18.0	
MN-A	♀	6	43	11.2	2.2	0.3	20	7.0	15.0	
	♂	6	19	11.6	2.3	0.5	19	8.0	16.0	
Nucleus	♀	6	43	3.4	1.0	0.1	27	3.0	6.0	
	♂	6	19	3.5	0.6	0.2	19	3.0	5.0	
Flagellum	♂	6	19	13.8	3.2	0.7	23	8.0	18.0	
	♀	6	43	14.7	3.0	0.5	20	8.0	19.5	

Table 11a. Comparison of trypanosome size (in mμ) between males and females of S. columbianus experimentally infected with the trypanosome strain from S. richardsonii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	3	24	44.0	2.7	0.6	6	38.0	51.5	
	♀	5	59	45.4	3.1	0.4	7	37.0	50.5	
Width	♂	3	24	2.4	0.5	0.1	21	2.0	3.0	
	♀	5	59	2.5	0.5	0.1	20	1.5	3.0	
P-K	♀	5	59	3.9	0.9	0.1	23	2.0	7.0	
	♂	3	24	4.2	0.7	0.2	17	3.0	5.0	
K-MN	♂	3	24	15.4	1.2	0.3	8	13.5	18.0	
	♀	5	59	15.7	1.7	0.2	11	12.0	19.0	
MN-A	♂	3	24	10.8	1.7	0.3	16	7.0	13.5	
	♀	5	59	11.4	1.9	0.3	17	7.0	16.5	
Nucleus	♀	5	59	3.6	0.6	0.1	17	3.0	5.0	
	♂	3	24	3.8	0.6	0.1	16	2.0	4.5	
Flagellum	♂	3	24	13.6	2.0	0.4	15	9.0	18.0	
	♀	5	59	14.4	2.7	0.4	19	6.0	19.5	

Table 11b. Comparison of trypanosome size (in mμ) between males and females of S. lateralis experimentally infected with the trypanosome strain from S. richardsonii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♀	3	109	42.9	3.3	0.3	8	31.5	48.5	
	♂	2	51	43.2	3.0	0.4	7	35.0	50.0	
Width	♀	3	109	2.2	0.5	0.1	23	1.5	3.0	
	♂	2	51	2.3	0.5	0.1	22	1.5	3.0	
P-K	♀	3	109	4.0	0.7	0.1	18	2.0	6.0	
	♂	2	51	4.0	0.5	0.1	13	3.0	5.0	
K-MN	♂	2	51	15.1	1.5	0.2	10	12.0	18.0	
	♀	3	109	15.5	1.4	0.1	9	13.0	19.0	
MN-A	♀	3	109	9.8	2.5	0.2	26	4.0	16.0	
	♂	2	51	10.7	2.2	0.3	21	6.0	15.0	
Nucleus	♂	2	51	4.3	0.7	0.1	16	3.0	6.0	
	♀	3	109	4.4	0.9	0.1	20	3.0	7.0	
Flagellum	♂	2	51	13.6	2.0	0.3	15	9.0	18.0	
	♀	3	109	13.7	3.0	0.3	22	6.0	20.0	

Table 11c. Comparison of trypanosome size (in mμ) between males and females of S. richardsonii experimentally infected with the trypanosome strain from S. richardsonii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♀	6	141	45.1	2.6	0.2	6	35.0	51.0	
	♂	3	86	45.9	2.5	0.3	5	36.0	51.0	
Width	♂	3	86	2.7	0.5	0.1	19	1.5	3.0	
	♀	6	141	2.7	0.5	0.0	19	1.5	3.0	
P-K	♀	6	141	3.9	0.9	0.1	23	1.5	6.0	
	♂	3	86	4.0	0.8	0.1	20	1.5	6.0	
K-MN	♂	3	86	16.2	1.4	0.2	9	13.0	19.0	
	♀	6	141	16.2	1.3	0.1	8	12.0	20.0	
MN-A	♂	3	86	11.4	2.0	0.2	18	7.0	18.0	
	♀	6	141	11.4	2.3	0.2	20	4.5	18.0	
Nucleus	♂	3	86	4.3	0.9	0.1	21	3.0	7.0	
	♀	6	141	4.6	0.8	0.1	17	3.0	7.0	
Flagellum	♀	6	141	13.6	2.5	0.2	18	7.0	24.0	
	♂	3	86	14.3	2.0	0.2	14	9.0	19.0	

Table 11d. Comparison of trypanosome size (in mμ) between males and females of S. undulatus experimentally infected with the trypanosome strain from S. richardsonii.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	1	75	44.8	2.3	0.3	5	37.5	50.0	|
	♀	1	6	47.0	1.3	0.5	33	46.0	49.0	
Width	♂	1	75	2.7	0.5	0.1	19	2.0	4.0	|
	♀	1	6	3.0	0.0	0.0	0	3.0	3.0	
P-K	♂	1	75	3.8	0.8	0.1	21	2.0	6.0	|
	♀	1	6	4.6	0.5	0.2	11	4.0	5.0	
K-MN	♂	1	75	15.4	1.5	0.2	10	10.0	18.0	
	♀	1	6	17.3	1.0	0.4	6	16.0	19.0	
MN-A	♀	1	6	10.5	2.8	1.1	27	6.0	14.0	|
	♂	1	75	10.9	1.8	0.2	17	6.0	15.0	
Nucleus	♂	1	75	4.1	0.7	0.1	17	3.0	6.0	
	♀	1	6	5.1	0.5	0.2	10	4.5	6.0	
Flagellum	♀	1	6	14.6	2.5	1.0	17	12.0	18.0	|
	♂	1	75	14.8	2.5	0.3	17	7.5	20.0	

Table 11e. Comparison of trypanosome size (in mμ) between male and female white rats experimentally infected with T. lewisi.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♀	2	80	39.8	4.5	0.5	11	22.5	51.0	
	♂	1	20	42.4	3.2	0.7	8	36.0	48.0	
Width	♀	2	80	3.2	0.8	0.1	25	2.0	6.0	
	♂	1	20	3.2	0.5	0.1	16	2.0	4.0	
P-K	♀	2	80	4.3	1.9	0.2	44	2.0	12.0	
	♂	1	20	5.8	0.7	0.2	12	4.5	7.0	
K-MN	♀	2	80	14.7	1.7	0.2	12	7.5	18.0	
	♂	1	20	16.3	1.6	0.4	10	12.0	19.5	
MN-A	♀	2	80	9.4	2.0	0.2	21	3.0	13.0	
	♂	1	20	9.5	1.6	0.4	17	6.0	12.0	
Nucleus	♀	2	80	3.7	0.7	0.1	19	2.0	5.0	
	♂	1	20	3.9	0.6	0.1	15	3.0	4.5	
Flagellum	♂	1	20	10.8	2.4	0.5	22	6.0	16.5	
	♀	2	80	11.5	2.3	0.3	20	7.0	22.0	

Table 11f. Comparison of trypanosome size (in mμ) between male and female white mice experimentally infected with T. musculi.

Measurement	Host sex	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	♂	4	60	41.6	4.4	0.6	11	30.0	49.5	
	♀	3	41	41.8	4.6	0.7	11	33.5	51.0	
Width	♀	3	41	3.5	0.8	0.1	23	2.0	5.0	
	♂	4	60	3.7	0.9	0.1	24	2.0	6.0	
P-K	♀	3	41	7.7	2.6	0.4	34	3.0	13.0	
	♂	4	60	8.0	2.4	0.3	30	4.5	12.0	
K-MN	♂	4	60	10.2	1.4	0.2	14	7.5	13.5	
	♀	3	41	10.2	1.5	0.2	15	7.0	13.5	
MN-A	♀	3	41	13.4	1.9	0.3	14	10.0	16.5	
	♂	4	60	13.9	2.7	0.4	19	8.0	19.0	
Nucleus	♀	3	41	4.1	0.6	0.1	15	3.0	6.0	
	♂	4	60	4.1	0.6	0.1	15	3.0	6.0	
Flagellum	♂	4	60	9.4	2.4	0.3	26	4.0	15.0	
	♀	3	41	10.4	2.1	0.3	20	7.5	15.0	

Table 12. Comparison of trypanosome size (in mμ) from S. richardsonii (R) and S. tridecemlineatus (T). Both host species were experimentally infected with equal portions of inoculum containing the trypanosome strain from S. richardsonii.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	T	3	67	39.3	2.4	0.3	6	32.5	44.5	
	R	4	91	44.9	2.6	0.3	6	38.0	51.0	
Width	T	3	67	2.6	0.5	0.1	19	1.5	3.0	
	R	4	91	2.7	0.5	0.1	16	2.0	3.0	
P-K	T	3	67	3.6	0.9	0.1	25	2.0	6.0	
	R	4	91	3.9	0.9	0.1	23	2.0	6.0	
K-MN	T	3	67	13.8	1.3	0.2	9	12.0	16.0	
	R	4	91	16.2	1.4	0.2	9	12.0	18.0	
MN-A	T	3	67	9.3	1.8	0.2	19	5.0	13.5	
	R	4	91	11.7	2.3	0.2	19	5.0	18.0	
Nucleus	T	3	67	4.4	1.0	0.1	24	3.0	6.0	
	R	4	91	4.6	0.9	0.1	20	3.0	7.0	
Flagellum	T	3	67	12.7	2.3	0.3	18	7.0	18.0	
	R	4	91	13.2	2.6	0.3	20	7.0	24.0	

Table 13. Comparison of trypanosome size (in mμ) from S. columbianus (C) and S. lateralis (L). Both host species were experimentally infected with equal portions of inoculum containing the trypanosome strain from S. richardsonii.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	L	5	160	43.0	3.2	0.3	7	31.5	50.0	
	C	5	44	43.6	2.7	0.4	6	37.0	51.5	
Width	L	5	160	2.2	0.5	0.0	24	1.5	3.0	
	C	5	44	2.4	0.5	0.1	21	1.5	3.0	
P-K	C	5	44	3.8	0.8	0.1	21	2.0	6.0	
	L	5	160	4.0	0.8	0.1	20	2.0	6.0	
K-MN	L	5	160	15.3	1.5	0.1	9	12.0	19.0	
	C	5	44	15.5	1.5	0.2	10	12.0	18.0	
MN-A	L	5	160	10.1	2.4	0.2	24	4.0	16.0	
	C	5	44	10.7	1.9	0.3	18	7.0	16.5	
Nucleus	C	5	44	3.9	0.6	0.1	15	3.0	5.0	
	L	5	160	4.4	0.8	0.1	19	3.0	6.0	
Flagellum	C	5	44	13.6	2.5	0.4	18	6.0	18.0	
	L	5	160	13.7	2.7	0.2	19	6.0	20.0	

Table 14. Comparison of trypanosome size (in mμ) from S. franklinii (F) and S. undulatus (U). Both host species were experimentally infected with equal portions of inoculum containing the trypanosome strain from S. richardsonii.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	F	1	12	41.8	2.7	0.8	6	38.0	44.5	
	U	2	81	45.0	2.3	0.3	5	40.0	50.0	
Width	F	1	12	2.5	0.5	0.2	21	2.0	3.0	
	U	2	81	2.7	0.5	0.1	18	2.0	3.0	
P-K	F	1	12	3.3	0.7	0.2	22	2.0	4.5	
	U	2	81	3.8	0.8	0.1	20	2.0	6.0	
K-MN	F	1	12	15.2	1.7	0.5	11	13.0	19.5	
	U	2	81	15.5	1.5	0.2	10	10.0	19.0	
MN-A	F	1	12	9.4	1.6	0.5	17	6.0	11.0	
	U	2	81	10.9	1.9	0.2	17	6.0	15.0	
Nucleus	F	1	12	4.0	0.9	0.3	23	3.0	6.0	
	U	2	81	4.1	0.7	0.1	17	3.0	6.0	
Flagellum	F	1	12	14.0	2.6	0.7	18	9.0	19.0	
	U	2	81	14.8	2.5	0.3	17	7.5	20.0	

Table 15. Comparison of trypanosome size (in mμ) from S. columbianus (C) and S. franklinii (F). Both host species were experimentally infected with equal portions of inoculum containing the trypanosome strain from S. richardsonii.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	F	2	54	44.5	2.4	0.3	5	37.0	48.0	
	C	3	39	46.6	2.6	0.4	6	38.0	52.0	
Width	F	2	54	2.4	0.5	0.1	21	1.5	3.0	I
	C	3	39	2.6	0.5	0.1	20	2.0	3.0	
P-K	F	2	54	3.9	0.7	0.1	17	3.0	6.0	I
	C	3	39	4.2	0.9	0.2	22	3.0	7.0	
K-MN	F	2	54	15.1	1.4	0.2	9	13.0	18.0	I
	C	3	39	15.7	1.7	0.3	11	13.0	19.0	
MN-A	F	2	54	10.9	1.9	0.3	18	7.0	14.0	I
	C	3	39	11.8	1.6	0.3	13	9.0	15.0	
Nucleus	C	3	39	3.4	0.6	0.1	18	2.0	4.5	
	F	2	54	3.8	0.7	0.1	18	3.0	6.0	
Flagellum	F	2	54	14.7	2.5	0.3	17	7.5	19.0	I
	C	3	39	14.8	2.5	0.4	17	9.0	19.5	

Table 16. Comparison of trypanosome size (in mμ) from S. columbianus (C) and S. tridecemlineatus (T). Both host species were experimentally infected with equal portions of inoculum containing the trypanosome strain from a naturally infected S. columbianus individual.

Measurement	Host species	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	T	1	21	40.4	2.6	0.6	6	33.5	44.5	
	C	1	47	43.8	4.0	0.6	9	33.0	50.0	
Width	T	1	21	2.3	0.6	0.1	26	1.5	3.0	
	C	1	47	2.5	0.5	0.1	20	1.5	3.0	
P-K	T	1	21	3.6	1.0	0.2	28	2.0	6.0	
	C	1	47	4.6	0.9	0.1	20	3.0	6.0	
K-MN	T	1	21	13.6	1.5	0.3	11	10.5	16.0	
	C	1	47	15.2	1.8	0.3	12	10.5	18.0	
MN-A	T	1	21	10.3	1.5	0.3	15	7.0	12.0	
	C	1	47	11.6	2.5	0.4	22	7.0	16.0	
Nucleus	T	1	21	3.7	0.6	0.1	16	3.0	4.5	
	C	1	47	4.0	0.7	0.1	18	3.0	6.0	
Flagellum	C	1	47	12.6	2.8	0.4	22	6.0	19.5	
	T	1	21	12.9	2.0	0.4	16	9.0	16.5	

Table 17a. Comparison of trypanosome size (in mμ) among the three stages of infection in S. columbianus experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	8	38	44.4	2.9	0.5	7	37.0	50.0	
	Dec.	5	12	45.1	3.1	0.9	7	41.5	51.5	
	Term.	7	33	45.6	3.0	0.5	7	39.5	50.5	
Width	Dec.	5	12	2.3	0.5	0.1	21	2.0	3.0	
	Inc.	8	38	2.5	0.5	0.1	21	2.0	3.0	
	Term.	7	33	2.6	0.5	0.1	20	1.5	3.0	
P-K	Term.	7	33	3.8	0.7	0.1	18	3.0	5.0	
	Dec.	5	12	4.0	0.8	0.2	19	2.0	5.0	
	Inc.	8	38	4.2	1.0	0.2	25	2.0	7.0	
K-MN	Inc.	8	38	15.0	1.5	0.2	10	12.0	19.0	
	Term.	7	33	16.1	1.5	0.3	10	13.0	19.0	
	Dec.	5	12	16.2	1.4	0.4	9	14.0	18.0	
MN-A	Dec.	5	12	10.8	1.9	0.6	18	7.5	14.0	
	Inc.	8	38	11.2	1.8	0.3	16	7.0	16.5	
	Term.	7	33	11.5	1.9	0.3	16	7.5	15.0	
Nucleus	Inc.	8	38	3.5	0.6	0.1	18	2.0	4.5	
	Term.	7	33	3.7	0.7	0.1	18	2.0	5.0	
	Dec.	5	12	3.8	0.6	0.2	16	3.0	4.5	
Flagellum	Inc.	8	38	14.1	3.0	0.5	21	6.0	19.5	
	Dec.	5	12	14.1	1.8	0.5	12	12.0	18.0	
	Term.	7	33	14.3	2.2	0.4	15	10.0	18.0	

Table 17b. Comparison of trypanosome size (in mμ) among the two stages of infection in S. franklinii experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	3	40	43.6	2.9	0.5	7	37.0	48.0	
	Dec.	3	26	44.5	2.1	0.4	5	39.5	48.0	
Width	Inc.	3	40	2.4	0.5	0.1	21	1.5	3.0	
	Dec.	3	26	2.5	0.5	0.1	21	2.0	3.0	
P-K	Dec.	3	26	3.8	0.7	0.1	18	3.0	5.0	
	Inc.	3	40	3.9	0.7	0.1	19	3.0	6.0	
K-MN	Inc.	3	40	14.7	1.3	0.2	9	12.0	18.0	
	Dec.	3	26	15.8	1.3	0.3	8	13.0	19.5	
MN-A	Dec.	3	26	9.9	1.7	0.3	17	7.0	13.0	
	Inc.	3	40	11.0	2.0	0.3	18	6.0	15.0	
Nucleus	Dec.	3	26	3.8	0.8	0.2	20	3.0	6.0	
	Inc.	3	40	3.9	0.7	0.1	19	3.0	6.0	
Flagellum	Inc.	3	40	14.3	2.3	0.4	16	7.5	18.0	
	Dec.	3	26	15.1	2.7	0.5	18	12.0	19.0	

Table 17c. Comparison of trypanosome size (in mμ) among the two stages of infection in S. lateralis experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	5	120	42.9	3.1	0.3	7	33.5	50.0	
	Dec.	4	40	43.2	3.4	0.5	8	31.5	48.5	
Width	Dec.	4	40	2.1	0.5	0.1	22	1.5	3.0	
	Inc.	5	120	2.3	0.5	0.1	24	1.5	3.0	
P-K	Dec.	4	40	3.9	0.7	0.1	18	2.0	5.0	
	Inc.	5	120	4.0	0.8	0.1	20	3.0	6.0	
K-MN	Inc.	5	120	15.3	1.5	0.1	10	12.0	19.0	
	Dec.	4	40	15.3	1.3	0.2	9	13.0	17.0	
MN-A	Dec.	4	40	9.0	2.1	0.3	23	6.0	15.0	
	Inc.	5	120	10.4	2.4	0.2	23	5.0	16.0	
Nucleus	Dec.	4	40	4.2	0.8	0.1	20	2.0	7.0	
	Inc.	5	120	4.4	0.8	0.1	19	3.0	6.0	
Flagellum	Inc.	5	120	13.3	2.5	0.2	19	7.0	19.0	
	Dec.	4	40	15.0	2.7	0.4	18	6.0	20.0	

Table 17d. Comparison of trypanosome size (in mμ) among the three stages of infection in S. richardsonii experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	9	44	44.6	2.2	0.3	5	38.0	48.0	
	Dec.	9	52	45.2	2.7	0.4	6	39.0	50.0	
	Term.	9	131	45.8	2.6	0.2	6	38.0	51.0	
Width	Inc.	9	44	2.7	0.5	0.1	18	1.5	3.0	
	Term.	9	131	2.7	0.5	0.0	18	1.5	3.0	
	Dec.	9	52	2.7	0.5	0.1	16	2.0	3.0	
P-K	Dec.	9	52	3.8	0.8	0.1	21	2.0	5.0	
	Term.	9	131	3.9	0.8	0.1	21	1.5	6.0	
	Inc.	9	44	4.3	0.9	0.1	20	3.0	6.0	
K-MN	Inc.	9	44	15.9	1.3	0.2	8	13.0	18.0	
	Dec.	9	52	16.2	1.4	0.2	8	12.0	19.5	
	Term.	9	131	16.3	1.3	0.1	8	13.5	20.0	
MN-A	Inc.	9	44	10.9	2.3	0.4	21	6.0	16.0	
	Dec.	9	52	11.0	2.2	0.3	20	4.5	16.0	
	Term.	9	131	11.7	2.1	0.2	18	8.0	18.0	
Nucleus	Term.	9	131	4.4	0.9	0.1	20	3.0	7.0	
	Inc.	9	44	4.4	0.9	0.1	21	4.0	6.0	
	Dec.	9	52	4.7	0.8	0.1	17	4.0	7.0	
Flagellum	Inc.	9	44	13.4	2.4	0.4	18	8.0	19.5	
	Term.	9	131	14.0	2.2	0.2	16	8.0	19.0	
	Dec.	9	52	14.2	2.7	0.4	19	9.0	19.0	

Table 17e. Comparison of trypanosome size (in mμ) among the three stages of infection in S. tridecemlineatus experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	3	31	39.1	2.3	0.4	6	32.5	43.0	
	Dec.	3	32	39.5	2.3	0.4	6	33.0	45.0	
	Term.	1	4	39.9	4.1	2.1	10	34.5	44.0	
Width	Dec.	3	32	2.6	0.5	0.1	21	1.5	3.0	
	Inc.	3	31	2.7	0.5	0.1	18	2.0	3.0	
	Term.	1	4	3.0	0.0	0.0	0	3.0	3.0	
P-K	Dec.	3	32	3.3	0.8	0.1	24	2.0	5.0	
	Term.	1	4	3.9	1.0	0.5	27	3.0	5.0	
	Inc.	3	31	3.9	0.9	0.2	23	2.0	6.0	
K-MN	Dec.	3	32	13.7	1.3	0.2	9	12.0	16.0	
	Term.	1	4	13.8	1.5	0.8	11	12.0	15.0	
	Inc.	3	31	13.9	1.2	0.2	9	12.0	16.0	
MN-A	Term.	1	4	8.8	2.8	1.4	31	6.0	12.0	
	Dec.	3	32	9.1	1.4	0.2	15	6.0	12.0	
	Inc.	3	31	9.5	2.1	0.4	22	5.0	13.5	
Nucleus	Dec.	3	32	4.3	1.1	0.2	27	3.0	6.0	
	Inc.	3	31	4.4	0.9	0.2	21	3.0	6.0	
	Term.	1	4	4.9	0.8	0.4	15	4.5	6.0	
Flagellum	Inc.	3	31	11.8	2.2	0.4	18	7.0	16.0	
	Dec.	3	32	13.5	2.0	0.4	15	9.0	18.0	
	Term.	1	4	13.5	3.0	1.5	22	12.0	18.0	

Table 17f. Comparison of trypanosome size (in mμ) among the three stages of infection in S. undulatus experimentally infected with the strain from S. richardsonii.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Dec.	1	30	44.8	1.8	0.3	4	42.0	47.0	
	Inc.	2	27	44.8	2.3	0.0	5	40.0	49.0	
	Term.	1	24	45.5	2.8	0.6	6	37.5	50.0	
Width	Dec.	1	30	2.6	0.5	0.1	19	2.0	3.0	
	Term.	1	24	2.6	0.6	0.1	22	2.0	4.0	
	Inc.	2	27	2.9	0.3	0.1	11	2.0	3.0	
P-K	Term.	1	24	3.3	0.7	0.1	20	2.0	4.5	
	Dec.	1	30	3.9	0.6	0.1	15	3.0	5.0	
	Inc.	2	27	4.3	0.8	0.2	18	4.0	6.0	
K-MN	Dec.	1	30	15.0	1.4	0.3	10	13.0	18.0	
	Inc.	2	27	15.6	1.8	0.4	12	10.0	19.0	
	Term.	1	24	16.1	1.1	0.2	7	15.0	18.0	
MN-A	Term.	1	24	10.5	1.9	0.4	18	6.0	12.0	
	Inc.	2	27	10.7	1.8	0.4	17	6.0	14.0	
	Dec.	1	30	11.4	2.0	0.4	17	7.0	15.0	
Nucleus	Dec.	1	30	4.0	0.6	0.1	16	3.0	6.0	
	Term.	1	24	4.0	0.8	0.2	20	3.0	6.0	
	Inc.	2	27	4.4	0.6	0.1	13	4.0	6.0	
Flagellum	Inc.	2	27	14.3	2.1	0.4	15	10.0	19.0	
	Dec.	1	30	14.5	2.2	0.4	15	11.0	19.5	
	Term.	1	24	15.6	3.1	0.6	20	7.5	20.0	

Table 17g. Comparison of trypanosome size (in mμ) among the three stages of T. lewisi infection in experimentally infected white rats.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets 1	Non-significant sets 2
Length	Term.	1	30	39.8	3.1	0.6	8	32.0	44.5		
	Inc.	3	49	40.6	4.3	0.6	11	31.5	51.0		
	Dec.	1	21	40.6	6.0	1.3	15	22.5	49.0		
Width	Term.	1	30	3.0	0.6	0.1	19	2.0	4.0		
	Dec.	1	21	3.3	0.9	0.2	26	2.0	6.0		
	Inc.	3	49	3.3	0.7	0.1	22	2.0	6.0		
P-K	Term.	1	30	3.6	0.7	0.1	19	2.0	4.5		
	Dec.	1	21	4.6	2.4	0.5	52	3.0	12.0		
	Inc.	3	49	5.2	1.8	0.3	35	2.0	12.0		
K-MN	Dec.	1	21	14.7	2.4	0.5	16	7.5	18.0		
	Term.	1	30	14.7	1.3	0.2	9	12.0	18.0		
	Inc.	3	49	15.3	1.8	0.3	12	12.0	19.5		
MN-A	Inc.	3	49	9.1	2.0	0.3	22	3.0	12.0		
	Dec.	1	21	9.5	2.3	0.5	24	4.5	13.5		
	Term.	1	30	9.7	1.4	0.3	14	7.5	13.0		
Nucleus	Term.	1	30	3.6	0.7	0.1	20	3.0	5.0		
	Inc.	3	49	3.8	0.7	0.1	19	2.0	5.0		
	Dec.	1	21	3.8	0.7	0.2	19	3.0	5.0		
Flagellum	Inc.	3	49	10.9	2.0	0.3	19	6.0	16.0		
	Term.	1	30	11.8	1.8	0.3	15	7.0	15.0		
	Dec.	1	21	12.0	3.4	0.7	28	7.5	22.0		

Table 17h. Comparison of trypanosome size (in mμ) between the two stages of T. musculi infection in experimentally infected white mice.

Measurement	Stage	NH	NT	Mean	S.D.	S.E.	C.V.	Range Lo	Range Hi	Non-significant sets
Length	Inc.	10	90	41.6	4.7	0.5	11	30.0	51.0	
	Dec.	10	56	42.3	3.4	0.5	8	36.0	48.5	
Width	Dec.	10	56	3.5	0.8	0.1	22	2.0	6.0	
	Inc.	10	90	3.7	0.9	0.1	24	2.0	6.0	
P-K	Dec.	10	56	7.8	2.2	0.3	28	4.0	12.0	
	Inc.	10	90	8.0	2.7	0.3	34	3.0	13.0	
K-MN	Inc.	10	90	10.1	1.7	0.2	16	7.5	13.5	
	Dec.	10	56	10.3	1.2	0.2	12	9.0	13.0	
MN-A	Inc.	10	90	13.4	2.7	0.3	20	8.0	18.0	
	Dec.	10	56	14.0	1.9	0.3	14	11.0	18.0	
Nucleus	Dec.	10	56	4.0	0.6	0.1	15	3.0	6.0	
	Inc.	10	90	4.2	0.6	0.1	15	3.0	6.0	
Flagellum	Inc.	10	90	10.0	2.5	0.3	25	4.0	17.0	
	Dec.	10	56	10.2	2.0	0.3	19	5.0	15.0	

Table 18. Correlation coefficients among the seven trypanosome body measurements for the five naturally infected species of ground squirrels.

Species		Measurement regions						
		L	W	P-K	K-MN	MN-A	N	F
S. columbianus	L	—						
	W	0.07	—					
NH:8	P-K	0.28*	-0.09	—				
NT:69	K-MN	0.43*	-0.00	-0.04	—			
	MN-A	0.49*	0.25*	0.15	-0.12	—		
	N	-0.22	0.07	-0.21	0.18	-0.23	—	
	F	0.40*	-0.12	-0.21	0.06	-0.40*	-0.07	—
S. franklinii	L	—						
	W	-0.27	—					
NH:3	P-K	0.61*	-0.32	—				
NT:24	K-MN	0.54*	-0.38	0.63*	—			
	MN-A	-0.18	0.03	-0.24	-0.33	—		
	N	-0.04	0.11	-0.08	0.02	-0.14	—	
	F	0.41*	0.15	-0.16	-0.30	-0.47*	0.07	—
S. richardsonii	L	—						
	W	-0.12	—					
NH:37	P-K	0.20*	-0.11	—				
NT:117	K-MN	0.23*	0.12	-0.20*	—			
	MN-A	0.36*	0.11	0.09	-0.03	—		
	N	-0.01	0.08	-0.03	0.25*	-0.12	—	
	F	0.47*	-0.22*	-0.15	-0.13	-0.53*	-0.00	—
S. tridecem-lineatus	L	—						
	W	-0.50	—					
NH:3	P-K	-0.03	0.02	—				
NT:15	K-MN	0.39	-0.41	-0.21	—			
	MN-A	0.09	-0.10	0.21	-0.28	—		
	N	0.21	-0.49	0.28	0.26	0.17	—	
	F	0.52*	-0.09	-0.33	0.02	-0.63*	-0.19	—
S. undulatus	L	—						
	W	0.03	—					
NH:12	P-K	0.25	0.18	—				
NT:62	K-MN	0.63*	-0.15	-0.14	—			
	MN-A	0.36*	0.26*	0.23	0.08	—		
	N	0.12	0.04	0.14	0.32*	0.06	—	
	F	0.65*	-0.15	-0.14	0.35*	-0.37*	-0.08	—

*Significant at p = 0.05.

Table 19. Correlation coefficients among the seven trypanosome body measurements for the six species of ground squirrels experimentally infected with inoculum from S. richardsonii.

Species		Measurement regions						
		L	W	P-K	K-MN	MN-A	N	F
S. columbianus	L	—						
	W	0.25*	—					
NH:8	P-K	0.32*	0.03	—				
NT:83	K-MN	0.38*	0.21	-0.18	—			
	MN-A	0.28*	0.25*	0.25*	-0.22*	—		
	N	-0.21	-0.03	-0.08	0.10	-0.22	—	
	F	0.64*	-0.02	-0.04	0.05	-0.34*	-0.13	—
S. franklinii	L	—						
	W	0.01	—					
NH:3	P-K	0.13	0.09	—				
NT:66	K-MN	0.32*	0.11	-0.07	—			
	MN-A	0.14	-0.15	0.07	-0.38*	—		
	N	0.17	0.26*	0.17	0.19	0.05	—	
	F	0.64*	0.00	-0.16	0.11	-0.45*	0.08	—
S. lateralis	L	—						
	W	0.05	—					
NH:5	P-K	0.31*	-0.11	—				
NT:160	K-MN	0.41*	0.10	0.11	—			
	MN-A	0.41*	0.10	0.18*	-0.14	—		
	N	0.13	0.07	0.01	0.22*	0.09	—	
	F	0.51*	-0.06	-0.15	0.04	-0.40*	-0.05	—
S. richardsonii	L	—						
	W	0.09	—					
NH:9	P-K	0.36*	0.09	—				
NT:227	K-MN	0.50*	-0.01	0.03	—			
	MN-A	0.22*	0.12	-0.00	-0.17*	—		
	N	0.08	0.13	-0.01	0.22*	-0.02	—	
	F	0.48*	-0.04	0.03	0.12	-0.59*	-0.01	—
S. tridecem-lineatus	L	—						
	W	-0.10	—					
NH:3	P-K	0.17	0.10	—				
NT:67	K-MN	0.55*	-0.07	0.12	—			
	MN-A	0.21	0.08	-0.10	-0.09	—		
	N	0.07	-0.05	0.06	0.29*	-0.05	—	
	F	0.54*	-0.16	-0.20	0.06	-0.48*	-0.07	—

Table 19. (continued)

Species		Measurement regions						
		L	W	P-K	K-MN	MN-A	N	F
S. undulatus	L	—						
	W	0.00	—					
NH:2	P-K	0.04	0.21	—				
NT:81	K-MN	0.37*	-0.02	-0.12	—			
	MN-A	0.14	0.12	0.05	-0.27*	—		
	N	0.24*	-0.03	0.25*	0.22	0.17	—	
	F	0.57*	-0.15	-0.24*	-0.04	-0.49*	-0.13	—

*Significant at p = 0.05.

Table 20. Correlation coefficients among the seven trypanosome body measurements for white rats and white mice experimentally infected with T. lewisi and T. musculi, respectively.

Species		Measurement regions						
		L	W	P-K	K-MN	MN-A	N	F
T. lewisi	L	—						
	W	0.36*	—					
NH:3	P-K	0.51*	0.51*	—				
NT:100	K-MN	0.68*	0.05	0.11	—			
	MN-A	0.53*	0.10	0.08	0.37*	—		
	N	0.17	0.07	0.04	0.20	0.29*	—	
	F	0.50*	0.15	0.01	0.10	-0.18	-0.10	—
T. musculi	L	—						
	W	0.21*	—					
NH:10	P-K	0.66*	0.38*	—				
NT:146	K-MN	0.04	-0.34*	-0.42*	—			
	MN-A	0.59*	0.24*	0.33*	-0.17*	—		
	N	-0.11	-0.01	0.02	0.03	-0.17*	—	
	F	0.46*	-0.07	0.04	0.07	-0.23*	-0.06	—

*Significant at p = 0.05.